THE SHELL STRUCTURE OF SPIRIFERIDE BRACHIOPODA

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SYNOPSIS

By studying the growth and structure of the shell of *Spiriferina walcotti* (Sowerby), a standard for the skeletal fabric of the order Spiriferida has been erected. Apart from the development of the spiral brachidium, shell growth involving deposition of primary and secondary calcareous layers (and also, presumably, a periostracum) in *Spiriferina* appears to have been little different from that of living Terebratulida. In many stocks, however, including the Atrypacea, Dayiacea, Reticulariacea, Koninckinacea and some Athyridacea and Spiriferacea, a tertiary layer similar to that deposited in the living terebratulacean *Gryphus vitreus* (Born) has been identified. Apart from the development of peripheral tubercles in Thecospiridae and some Koninckinacea (which are both assigned to the Spiriferida) the shell structure of all remaining spire-bearers does not differ markedly from that of living Rhynchonellida or Terebratulida.

The ultrastructure of the spiral brachidia of a number of genera has been examined and two distinct growth patterns have been recognized. 'Single-sided' growth is characteristic of the athyrididine spiralium whereas 'double-sided' growth is characteristic of all other spiriferides examined. Consideration is given to the disposition of the spiriferide lophophore.

I. INTRODUCTION

The advent of the electron microscope has led to an upsurge in studies relating to the shell structure of living and fossil Brachiopoda. The most significant contribution to date, with respect to articulate Brachiopoda, has been that of Williams (1968a) in which it was shown that a triple division of the shell into periostracum, and primary and secondary calcareous layers, is characteristic of most members of this major class. By studying the soft tissues as well as the calcareous exoskeleton of living Rhynchonellida and Terebratulida, Williams was able to rationalize shell growth in terms of the secretory behaviour of individual outer epithelial cells. In dealing with the Spiriferida Williams (1968a : 31–34) referred briefly to the skeletal fabrics of a number of atrypidines, athyridines, retziidines and spiriferidines, showing that in general they possessed a shell ultrastructure similar in many ways to that found in Recent Rhynchonellida and Terebratulida, but it was outside the scope of that report to include a more detailed survey of the order. This paper is intended as a contribution towards a greater understanding of the processes of shell deposition within the phylum from both a functional and evolutionary standpoint.

To make sense of a comparative study of the shell fabrics of fossil Spiriferida, investigations must be based on a workable classification. In this exploratory survey the *Treatise* classification, as erected by Boucot, Johnson, Pitrat and Staton (1965) has been followed but only down to the rank of superfamily. As will be shown, below this level of classification trends in ultramicroscopic shell variation, as well as gross morphological distinctions, become less clearly defined.

The fact that no spiriferide genera (as far as is known) survive to the present day has necessitated the selection of a suitable fossil representative as a standard model for the skeletal fabric of the order. *Spiriferina walcotti* (Sowerby) fits this role well for, apart from being a member of the last surviving spiriferide stock, its mode of preservation is normally very good and adequate numbers of complete specimens may be readily collected and prepared for study. Consequently a complete section of this paper is devoted to a description of the shell structure of *Spiriferina walcotti* prior to consideration of the skeletal fabrics of the order as a whole.

One aspect of spiriferide morphology which has excited some interest in recent years has been the problem of establishing the nature and disposition of the lophophore which must have been supported by the calcareous spiralia. With this thought in mind, the structure of the spiralia of as many genera as possible has been studied and compared with the structure of the calcareous supports in living Terebratulida. Since the orientation of the lophophore in living Terebratulida can be determined in relation to the disposition of the ascending and descending branches of the calcareous loop, the possibilities of applying these findings to the Spiriferida have been investigated.

II. TECHNIQUE OF SPECIMEN PREPARATION

Both surfaces and sections of calcareous shells were examined under a Cambridge 'Stereoscan' scanning electron microscope. Initially specimens were embedded in Epon Araldite resin then cut and ground, first on a diamond grinder and then on fine grade (C600) silicon carbide paper. A relatively scratch-free finish was obtained by using a paste of Aloxite optical smoothing powder along with the silicon carbide paper. Surfaces prepared in this manner were finally polished on a cloth-covered disc which was impregnated with stannic oxide or slow-cutting polishing alumina. Before mounting, the embedded specimens were cut to a convenient area and thickness and ultrasonically cleaned for a few minutes in a mild detergent solution, then in acetone. Fragments of internal or external shell surfaces requiring investigation were cleaned in the same way. Once dry, specimens were mounted on aluminium stubs using a conductive adhesive (Lo-Kitt) then fixed on a rotatable table in a vacuum evaporator and coated with a thin deposit (about 0·03–0·05 μm in thickness) of gold/palladium alloy. A thin metallic coating of this nature is necessary when examining calcareous shell fragments in order to render the specimens conductive and prevent charge build-up.

All important 'Stereoscan' observations were recorded photographically. In certain cases it was found that the size of skeletal components, in particular secondary layer fibres, was such that individual 10 × 10 cm prints did not provide a sufficiently detailed overall view of the area under investigation. To overcome this lack of structural detail a montage of overlapping prints, which had been photographed at higher magnifications, was constructed. In general, a 20 per cent overlap was required to produce a reasonable match-up of corresponding features in adjacent prints.

All mounted specimens used in this study have been presented to the British Museum (Natural History) and retain the registered numbers BB 58878 to BB 59009.

III. SHELL STRUCTURE OF *SPIRIFERINA WALCOTTI* (SOWERBY)

Spiriferina walcotti (Sowerby) occurs within the British Lias and is especially common in the highly attenuated sequence of Lower Liassic rocks around Radstock and Bath. In this area, commonly referred to as the 'Radstock Shelf', the state of preservation of the shell is normally very good and complete specimens, with fully articulated valves, are abundant. It is convenient, therefore, to consider this species of the last surviving spiriferide genus as a model for the skeletal fabric of the order and, by studying the ultrastructure of its shell, reconstruct the morphology and disposition of its mantle. The restored species may then be used as a standard with which all other Spiriferida may be compared.

Tutcher & Trueman (1925 : 595) have given a detailed description of many fossiliferous localities within the Radstock area, though regrettably a number of sections and quarries listed by them are now overgrown with thick vegetation or filled in with earth and rubble. Fortunately Bowlditch Quarry (ST 668559) north of Radstock and Hodder's Quarry (ST 674584), Timsbury, both sources in the past of some of the finest specimens of *S. walcotti*, are still accessible. All specimens examined during the present investigation came from either one or other locality.

Before considering the microstructure of the shell of *S. walcotti*, it seems appropriate to describe the morphology of the shell because, as far as is known, no up-to-date account of the species is available. Certainly a knowledge of the morphology of exoskeletal outgrowths and their relationship with the shell is essential before the microstructure of critical sections can be fully understood. The following diagnosis supplements the descriptions given by Davidson (1852 : 25) and Hall & Clarke (1894 : 51) :

Shell moderately transverse in outline, with rounded cardinal extremities ; biconvex in profile, anterior commissure uniplicate, distinct fold and sulcus ; lateral slopes with distinct, rounded, simple costae ranging from 2 to 5 (modally 4) on each slope. Ventral interarea gently curved, dorsal interarea low ; both traversed by growth lines, fine striae intermittently developed normal to transverse growth lines. Triangular delthyrium, partly restricted by a pair of dental ridges (cf. Dunlop 1962 : 491) ; low triangular notothyrium. Surface further ornamented by concentric growth lines and numerous fine, tubular spines ; shell endopunctate.

Interior of pedicle valve with high, dorsally pointed median septum extending for almost half the length of the valve and bearing broad, well-defined adductor muscle scars ; diductor and ventral adjustor muscle scars impressed on valve floor on either side of median septum. Teeth prominent ; dental plates short, diverging from umbo and terminating on the valve floor just postero-laterally to the diductor muscle scars.

Interior of brachial valve with triangular cardinal process, usually striated parallel to the median plane, bounded laterally by posterior walls of inner socket ridges ; dorsal adjustor scars deeply impressed on the crural bases, situated just antero-laterally to the cardinal process and each bounded by an inner socket ridge. Crura broad, supporting laterally directed spires with as many as 15 convolutions ; primary lamellae united by single jugum ; anteriorly facing edges of spiral lamellae spinose ; two pairs of dorsal adductor muscle scars with the anterior pair more prominently inserted on floor of valve.

(a) The shell succession

(i) *Periostracum*

The chances of finding traces of the organic constituent of the shell of *Spiriferina* that are identifiable under the electron microscope are very small. However, amino-acids have been recovered by Jope (1965 : H161) from several spiriferide shells and it is highly likely that the organic parts of the exoskeletal succession were similar to those found in living species. In particular, a periostracum would have been necessary as a seeding sheet for the mineral part of the shell, and membranes must also have ensheathed the fibres of the secondary shell. Both constituents must have played a decisive part in determining the ultrastructure of the primary and secondary calcareous shell.

(ii) *Primary layer*

Although the external surface of the primary layer is finely granular a distinct lineation is visible with the long axes of the particles radially aligned (Pl. 1, fig. 1). At intervals of about 20 μm, fine concentric growth lines are superimposed on this fabric (Pl. 1, fig. 2) so that, whilst no remnant periostracal covering remains, an impression of its basal membrane is preserved. Anterior to the base of each spine the surface of the shell is dissected by a prominent longitudinal groove (Pl. 1, fig. 3) whilst several more conspicuous grooves, also aligned parallel to the long axis of the shell and spaced from 4 to 6 μm apart, are deflected around the posterior of the spine base (Pl. 1, fig. 4). If the dimensions of terminal faces of fibres situated around the periphery of the valve margins can be taken as a guide to the size of outer epithelial cells located close to the edge of the outer mantle lobe (about 5 μm wide), then it is reasonable to assume that the longitudinal grooves posterior to each spine base, being similarly spaced, correspond to the lateral boundaries of rows of cuboidal epithelium.

In mature specimens of *Spiriferina*, the thickness of the primary layer can vary from about 30 μm, close to the umbo, to 100 μm or more at the anterior commissure (Text-fig. 1). Since deposition of the primary layer is restricted to a narrow zone of outer epithelial cells located around the shell edge, the observed thickening of the primary layer can be interpreted as a progressive widening of this zone with age.

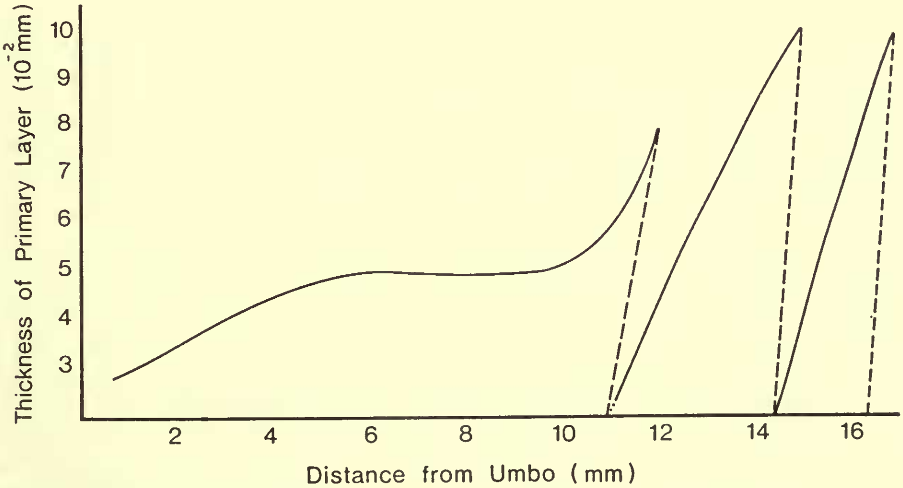

FIG. 1. Graph showing the increase in the thickness of the primary layer from umbo to anterior commissure in a brachial valve of *Spiriferina*. Broken lines denote regression planes of overlapping growth lamellae.

Unless the dimensions of newly proliferated cells increase drastically as the brachiopod approaches maturity, a widening of the zone of primary shell deposition must be accompanied by an overall increase in the number of cells involved in secreting that layer. If such is the case, the widening of the primary shell secretory zone must also reflect an increasing delay with age in the change-over to secondary shell deposition (cf. Williams 1971a : 58). Alternatively, primary layer thickening may be related to an increase in the marginal angle of the shell which may result from a reduction in the migration rate of cells in the conveyor-belt system of the outer mantle lobe.

In section, a twofold division of the primary layer is recognizable (Pl. 1, fig. 5). It is possible to distinguish between an outer, finely granular, porous part which gradually merges into a more compact inner portion composed of crystallites (averaging less than 10 μm in length) orientated with their long axes normal or posteriorly inclined to the isotopic boundary (Westbroek 1967 : 23) defining the junction between the primary and secondary shell layers. Electron micrographs of random, oblique sections of *Spiriferina* show that grain boundaries of primary layer crystallites are regularly found in continuity with the first-formed, inwardly convex boundaries of secondary layer fibres so that organic membranes, known to ensheath the latter, could also have extended deep within the primary layer. In radial sections, a faint banding is occasionally seen which runs posteriorly at a low angle from the external surface to the internal boundary with the secondary layer. The banding is considered to be depositional, and thus merits recognition as a superficial (isochronous) shell unit boundary, as defined by Westbroek. Such radial sections serve to establish the relationship between these surfaces and the calcareous skeletal constituents when the first formed fibres occur as long rods dipping gently towards the anterior shell edge. In addition, the crystallites of the primary layer are, in general, posteriorly inclined to the isotopic surfaces between the primary and secondary layers, but normal to the observed depositional banding.

As this twofold division of the primary layer is not characteristic of Recent Rhynchonellida and Terebratulida, it is possible that the textural variation is secondary in origin. If, for some unknown reason, the primary layer of *Spiriferina* were especially prone to recrystallization, the process would be confined within a space bounded externally by compacted grains of enclosing sediment and internally by the fibres of the secondary shell. Recrystallization normal to these two interfaces might then have given rise to two contrasting crystalline textures growing towards one another. However, specimens of the terebratulacean *Lobothyris punctata* (Sowerby), collected from the same localities as *Spiriferina*, exhibit a primary layer texture closely resembling that of living Terebratulida, whilst the fibres of the secondary shell of both species are in an identical state of preservation. Such evidence suggests that textural differences in the primary layer of *Spiriferina* are original.

The twofold nature of the primary shell is not unique to *Spiriferina*. Armstrong (1968a : 184), in describing the microstructure of the shell of the spiriferide *Subansiria* sp. from the Permian rocks of Queensland, Eastern Australia, distinguished within its primary layer an identical granular outer part and finely crystalline inner portion. Armstrong maintained that the boundaries between the primary layer components of *Subansiria* sp. are as distinctive as the inter-fibre junctions in the secondary shell.

Such a comparison prompted him to postulate the deposition of organic membranes around the crystals of the primary layer. The outer granular portion of the primary layer, he suggested, may have been the product of a transitional phase of organic–mineral deposition following the secretion of the periostracum and preceding formation of the more regular crystals.

Growth of the primary layer in Recent Rhynchonellida and Terebratulida, as described by Williams (1968a), could not account for the twofold structure of that layer in *Spiriferina*. In living articulates, the first formed seeds of calcite are secreted by cells situated at the tip of the outer mantle lobe onto an embedding protein cement comprising the innermost surface of the periostracum. Initially the seeds tend to be concentrated in zones separated by inwardly directed bars of periostracum and isolated from one another by membranous projections of the cells (microvilli) attached to the periostracum. As deposition continues, the crystallites grow and overlap one another across intercellular boundaries, but microvilli continue to permeate the primary layer to give its inner surface a highly porous appearance. However, observations recorded above suggest that, although growth of the primary layer of *Spiriferina* started in similar fashion with deposition of the first calcite crystallites onto an embedding protein sheet forming the internal surface of the periostracum, the crystallites did not quickly coalesce. Instead they were kept isolated from one another by a fine membranous web extending inwards from the periostracum and deposited simultaneously with the crystallites by the outer epithelial cells. As an increasingly thick wedge of primary layer was deposited, organic secretion became less prevalent and many connecting membranes became pinched out. Hence crystallites amalgamated with one another and imparted to the inner half of the layer a more homogeneous appearance. Finally at a certain distance from the shell edge, organic secretion became restricted to an arcuate sector of the secreting plasmalemma and deposition of the secondary layer began.

(iii) *Secondary layer*

The secondary shell layer is built up from orthodoxly stacked fibres. On the internal surface of the shell, the terminal faces of the overlapping fibres produce the standard secondary shell mosaic pattern (Pl. 1, fig. 6). Whilst secondary generative zones are known to occur in certain areas of the outer epithelium, the main zone of cell proliferation and fibre formation is located around the shell edge. In this area, the young fibres of *Spiriferina* with terminal faces no more than 5 μm wide grew normal to the commissure. The consistency of this initial growth direction is verified by examination of the external surface of specimens from which the primary layer has broken off during removal from the enclosing sediment. In such specimens, the freshly exposed trails of the secondary layer fibres are radially disposed over the entire shell surface. When young fibres of *Spiriferina* come to occupy a position up to about 100 μm behind the leading edge of the secondary shell mosaic, they become reorientated, broadly speaking, in a sub-parallel arc ; clockwise in the right half of the valve, anti-clockwise in the left.

Terminal faces of mature fibres are spatulate, normally 30 μm long and 15 μm at maximum width. However, on some parts of the inner shell surface, they may become elongate with long exposed trails. Other more drastic changes take place in those fibres underlying the muscle attachment areas, but these will be considered separately. Small localized convolutions in the form of spiral arcs and tight S-shaped patterns may be found in most parts of the shell. Similar minor modifications occur in the shells of a number of Recent articulates (Williams 1968a : 9) and are considered simply to reflect small epithelial adjustments in adjacent zones of the internal surface.

In gerontic forms, radial fibre growth around the commissure becomes less prevalent since the normal secretory regime in this area is disrupted by repeated mantle retractions. This particular aspect of mantle behaviour and shell deposition will, however, be dealt with separately.

(b) Punctation

The shell of *Spiriferina* is endopunctate. As in living Terebratulida, perfectly interlocking fibres of the secondary layer fashion and preserve the cylindroid shape of the canals which measure, on average, 30–40 μm in diameter. This is well displayed on the internal surfaces of *Spiriferina* where the advancing fibres are momentarily deflected from their paths of growth so as to sweep around the puncta, but thereafter continue on their previous course (Pl. 2, fig. 1). In some cases where a fibre trail lies directly in line with a caecum, the fibre may terminate on one side of the cavity and reappear, without any noticeable change in size or shape, on the side directly opposite. In section, the fibres on either side of the puncta arch outwards towards the primary layer (see Pl. 3). The puncta so defined do not run quite normal to the shell layers but slope anteriorly from the shell exterior at a steep angle of about 80 degrees. Within the umbonal region of the pedicle valve, groups of branching puncta are found. Towards the interior of the shell up to five discrete canals may merge into one central canal. Such branched puncta are considered to have formed as a result of the coalescence of originally discrete puncta due to extensive deposition of calcite in that part of the shell.

When viewed from the exterior, the puncta of *Spiriferina* usually break the surface of the primary layer, but in several cases fragmentary distal coverings, about 1 μm thick, were observed *in situ* (Pl. 2, fig. 2). This thin layer of primary shell material is perforated by densely distributed canals, each measuring approximately 500 nm in diameter (Pl. 2, fig. 3).

Since the perforate canopies covering the distal ends of puncta in *Spiriferina* are so unmistakably like those in living Terebratulida (MacKinnon 1971a), it seems certain that the puncta of *Spiriferina* must have accommodated caeca virtually identical in ultrastructure with those in living endopunctate brachiopods.

(c) Hollow spines

The micro-ornament visible on the exterior surface of *Spiriferina* consists of a variably dense concentration of hollow spines, on average 80 μm in diameter at their bases and tapering distally to about 35 μm, which project at low angles towards the commissure (Pl. 1, fig. 2). They are usually broken, but a few may remain more or less intact between costae where stalks up to 2 mm in length have been found. All spinose outgrowths are composed solely of primary shell material, but the narrow canals running through the spines, on average 30–40 μm wide in mature specimens, do not terminate at the primary/secondary shell layer boundary. Starting from the shell exterior, a canal can be traced running posteriorly parallel to the length of a spine until it reaches the spine base, whereupon it bends sharply through 90 degrees before passing through the remainder of the secondary layer (Text-fig. 2). Throughout the secondary layer, the walls of the canals are fashioned by fibre trails which are deflected around one side or the other in a manner identical to that found in puncta. On the inner shell surface, the cylindroid hollows forming both puncta and spine canals are indistinguishable. Although the distal ends of spines are broken off, no blocking up of canals due to subsequent shell deposition has been observed in the surviving basal parts.

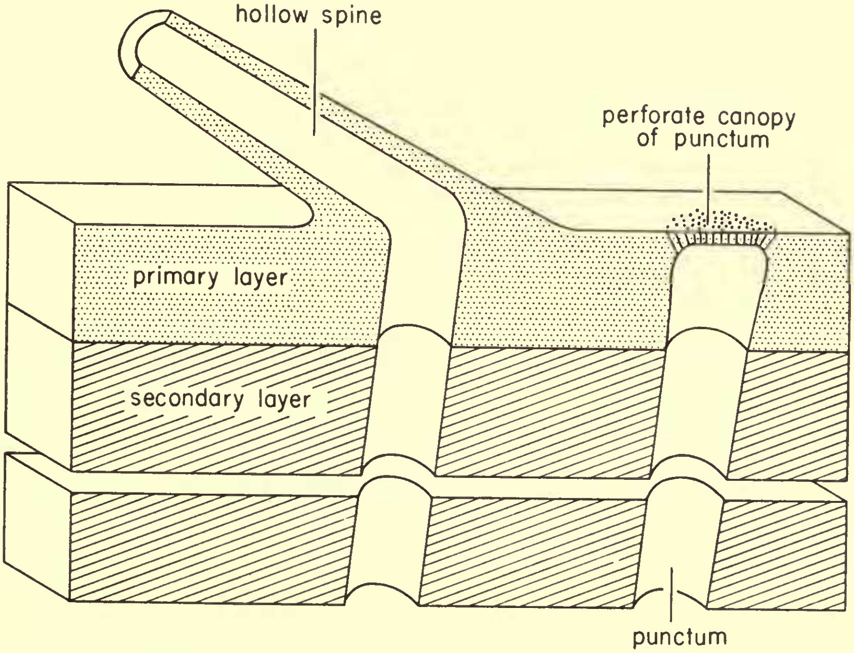

FIG. 2. Block diagram showing the relationship between a hollow spine, a punctum and the calcareous shell succession in *Spiriferina*. Anterior commissure of shell located beyond the left-hand margin of the diagram.

The density of distribution of spinose outgrowths is variable over the whole shell surface. Within 5 mm of the umbo, which incorporates the earliest formed parts of the shell, the surface density of hollow spines rarely exceeds 5 per mm². Around the commissure of mature specimens, however, the density is appreciably greater, rising to as much as 35 per mm². In general, the spines do not conform to any recognizable pattern on the shell exterior, but close to the anterior commissure of mature specimens where the concentration of spinose outgrowths is densest, localized groups of spines appear to be arranged 'in quincunx'. In such areas, a one-to-one correspondence exists between spine bases and puncta with the puncta set out in alternating rows between spine bases.

Clearly the spines were built up very quickly by the secretion of calcite in small circumferential generative zones of outer epithelium located close to the tip of the outer mantle lobe, but they did not continue to increase in length throughout life as happened in certain strophomenides. Whereas strophomenide spines continued to grow indefinitely with accretion of primary and secondary shell material (or were eventually sealed off), the spines of *Spiriferina* grew only during the period in which adjacent cells were employed in primary shell formation. Once the underlying epithelium changed to secreting the secondary layer, growth of the spines ceased.

The structure and distribution of the spines provide little indication of their function. Unlike the hollow spines of genera such as *Acanthothiris* (Rudwick 1965 : 610), and certain Siphonotretacea (Biernat and Williams 1971 : 429), the spines extending from the surface of *Spiriferina* were not long or large enough to have functioned efficiently as protective grilles. Even if the shell were closed, spines extending from both valves would not have intersected. Rudwick (1965 : 610) suggests that the hollow spines of *Acanthothiris* probably accommodated sensory organs which could have provided the brachiopod with effective 'early-warning' protection against potentially harmful agents in the environment. The tips of growing spines, however, would have been occupied by generative cells involved in the proliferation of new cells and the secretion of mucopolysaccharide and periostracum. Thus the presence of these external covers would surely have militated against any chemo-sensitivity of the tips of spines developed as extensions of the shells of any brachiopod, including *Spiriferina*. However, since the shell exterior is to a large extent free from boring organisms and any encrusting epifauna, it is possible that the function of the spines was protective. As Owen & Williams (1969 : 200) have pointed out, the typical brachiopod exterior seems frequently to attract a rich benthonic microfauna, consisting of bryozoans, sponges, algae etc. Obviously an irregular surface topography, broken up by spines, would tend to hinder and discourage the settlement of such organisms onto the surface of the periostracum.

(d) Concentric growth lines and mantle retraction

The presence of concentric growth lines on the outer surfaces of both valves is characteristic of a great number of Spiriferida. These are considered to be the result of a series of successive pauses or even complete breaks in deposition affecting the normal pattern of radial growth. In the past, palaeontologists have found sets of growth lines to be of great systematic value in recognizing a number of successive ontogenetic stages in many genera. Krans (1965 : 87), using a dry peel technique with carefully orientated sections, has made a study of the shell growth in a number of Devonian Spiriferida and has distinguished three main types of growth features. These are :

(1) *Slight flexures* where the shell layers are bent into a small kink due to a pause in radial growth whilst deposition of calcite continues.
(2) *Overlapping growth lamellae* where the primary and secondary shell layers are bent around to face posteriorly inwards before returning to normal radial growth.
(3) *Free growth lamellae* caused by a distinct break in deposition of calcite with a strip of mantle around the shell edge actually detaching itself from a part which it has already formed. In addition, the mantle undergoes an abrupt retraction before returning to the normal course of deposition.

Such observations are comparable with those made by Brunton (1969) and Williams (1971a) on Recent Rhynchonellida and Terebratulida, but the signs of depositional pauses or breaks described for *Spiriferina*, though similar, are not identical.

Minor fluctuations in the rate of shell deposition, as well as more drastic physiological changes in the secretory role of outer epithelial cells situated around the mantle edge, contributed to the appearance of a variety of concentric growth lines over most of the shell exterior. The finest, which are microscopic growth lines normally no more than 20 μm apart, are surface features unaccompanied by any differential thickening of the primary layer (Pl. 1, figs. 1, 2). Where there are slight flexures in the shell layers, each producing a concentric ridge in the order of 100 μm in amplitude, the primary layer is warped in a manner analogous to monoclinal folding, whereas the underlying fibres of the secondary layer are crowded together and display cross-sectional outlines different from those either in front of or behind the modified zone (Pl. 2, fig. 5). Most of the major overlapping shell units are found around the commissures of mature specimens. In radial section (Pl. 3), normal secondary layer fibres are bent sharply backwards against a line, posteriorly inclined, and running from the primary/secondary layer interface inwards towards the shell interior. Below this line, a series of lamellae, composed of primary shell material, are stacked one below the other so that their posterior ends are in continuity with the line of 'unconformity'. The lamellae are flat or slightly convex inwards and vary between 5 μm and 10 μm in thickness. Finally the lamellae pass inwards to a normal primary and secondary layer succession which extends anteriorly to the next major concentric growth line. Secondary layer fibres associated with major overlapping shell units are generally stacked with long axes parallel, and not at right angles, to the valve margins.

The frequency and spacing of the microscopic concentric growth lines suggest that they are remnants of the linear junctions between successive rows of outer epithelial cells as each in turn changed over from organic to mineral secretion. The slight flexures in the shell layers are produced by a change from radial to tangential growth which results in the radial growth vector being reduced to zero, whilst the growth vector normal to the shell edge is greatly increased. Calcite secretion does not stop and there is no retraction of the mantle, but the fibres located around the periphery of the shell tend to grow parallel and not at right angles to the shell edge. The major overlapping shell units which are found around the periphery of most mature individuals appear similar to the free growth lamellae of Krans (1965 : 88). When

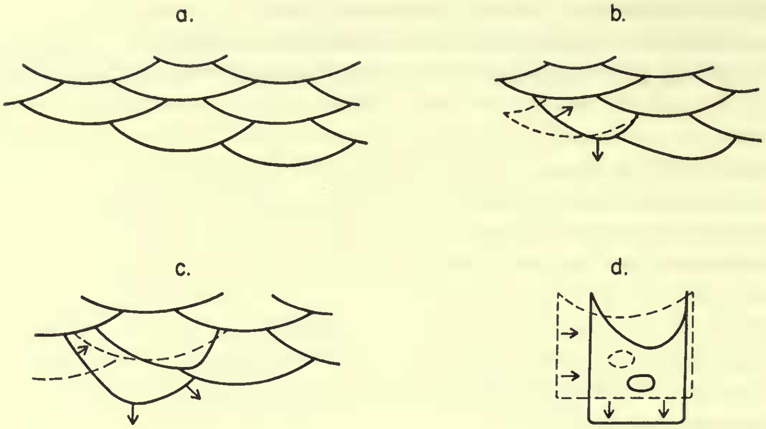

FIG. 3. a–c. Stylized drawings of transverse sections through secondary layer fibres showing how a series of slight changes in profile may produce a substantial overall displacement. d. Section through an outer epithelial cell showing how a lateral contraction will produce greater concavity in the secreting plasmalemma.

examined in greater detail, however, they are found to be the culmination of a series of minor mantle readjustments. The first stage in the formation of a new shell unit around the edge is brought about by a breakdown in the secretory regime of the underlying outer epithelium. This may be preceded by a slight posterior withdrawal of the outer mantle lobe, giving rise to a narrow zone of fibres which are bent round sharply on one another. It is remarkable how the gradual change in shape of a cell, and in particular its secreting plasmalemma, when combined with similar changes in adjacent cells, can give rise to macroscopic variations in the shell layers. A lateral contraction produces greater concavity in the secreting plasmalemma, hence the terminal face of the fibre secreted by it will become narrower and more highly convex (Text-fig. 3). The gross effect is to produce a lateral foreshortening and vertical thickening within the shell layer. The first major break in the secretory regime of the outer epithelium corresponds to a halt in the 'conveyor belt' system of cell proliferation and hence to a lapse in radial growth. Deposition continues normal to the plane of regression but the organic membranes secreted by arcuate strips of each outer epithelial cell are often pinched out. A gradual regression of the mantle edge follows with deposition of successive horizontal lamellae composed of primary shell. The lamellae are not stacked vertically one above the other, but are stepped progressively backwards. Between each regression plane there is a thin wedge of micritic material. Very probably the interlamellar spaces were occupied by organic material secreted by the mantle to assist in its backward slide. On the other hand, if deposition of periostracum were continuous at the mantle edge (as is highly likely) the spaces between the lamellae may have been occupied by folds of that protective outer cover which would have functioned as an ideal seeding sheet for each consecutive calcite lamina.

To produce a thickening of the shell in this manner, it is clear that the same outer epithelial cells must have undergone cyclical changes in secretory regime (Text-fig. 4). Initially involved in secreting the primary, then secondary, shell layers, they must have continually fluctuated between organic and inorganic episodes of deposition until the stage was reached where mantle retraction stopped and normal growth of the shell layers resumed.

(e) Muscle attachment areas

The areas of muscle attachment in *Spiriferina* are distributed similarly to those found in living articulates, except for the ventral adductor muscle fields which are situated on both sides of a large, pointed, ventral, median septum and not on the floor of the valve.

(i) *Pedicle valve*

The ventral diductor and adjustor muscle bases leave strong impressions on the valve floor, so that the ventral muscle scars are well defined (Pl. 2, fig. 4). Around the anterior margins of each scar, there is a prominent, anteriorly arcuate ridge (Pl. 2, fig. 4 ; Pl. 4, fig. 1) like that found around the anterior border of the ventral muscle scars of the Recent rhynchonellide *Notosaria nigricans* (Sowerby). It is built up from secondary layer fibres. Although the effects of fossilization tend to obscure the finer details of textural variations in the shell fabric, it is evident that the exposed parts of fibres on the posterior facing side of the ridge exhibit longer, more ragged trails than those comprising the crest of the ridge. Traced posteriorly from the ridge crest the exposed fibre trails are overlapped by fibres whose terminal faces exhibit a fairly well-developed mosaic pattern. The difference in growth direction of both sets of fibres is striking, which suggests that the zone of fibres overlapping the ridge grew quite independently of those which actually composed the ridge. Indeed, a significant lowering of the level of the valve floor behind the ridge and the existence of long, ragged, exposed trails on its posteriorly sloping side suggest that the outer epithelium in contact with that part of the ridge was resorbing and not depositing shell material. About 500 μm behind the ridge, the inner shell surface is cut up by a series of deeply impressed furrows, each measuring between 75–100 μm in width (Pl. 4, fig. 2). Within the ventral adjustor muscle field, the furrows run longitudinally and are generally separated from one another by narrow ridges of fibres exhibiting a fairly well-developed secondary shell mosaic (Pl. 4, fig. 3). Within the diductor muscle field, however, the anterior parts of the furrows bend round to face the median septum. In addition, groups of neighbouring furrows tend to merge together, unlike the adjustor scar, so that the outlines of the impressions appear flabellate.

The occurrence of a well-developed mosaic pattern within a muscle scar is unusual and has not been observed within the muscle scars of any Recent articulate. Generally a myotest shell fabric is quite distinct from the normal secondary shell mosaic pattern. The fact that fibres occurring within the elongate furrows of the muscle

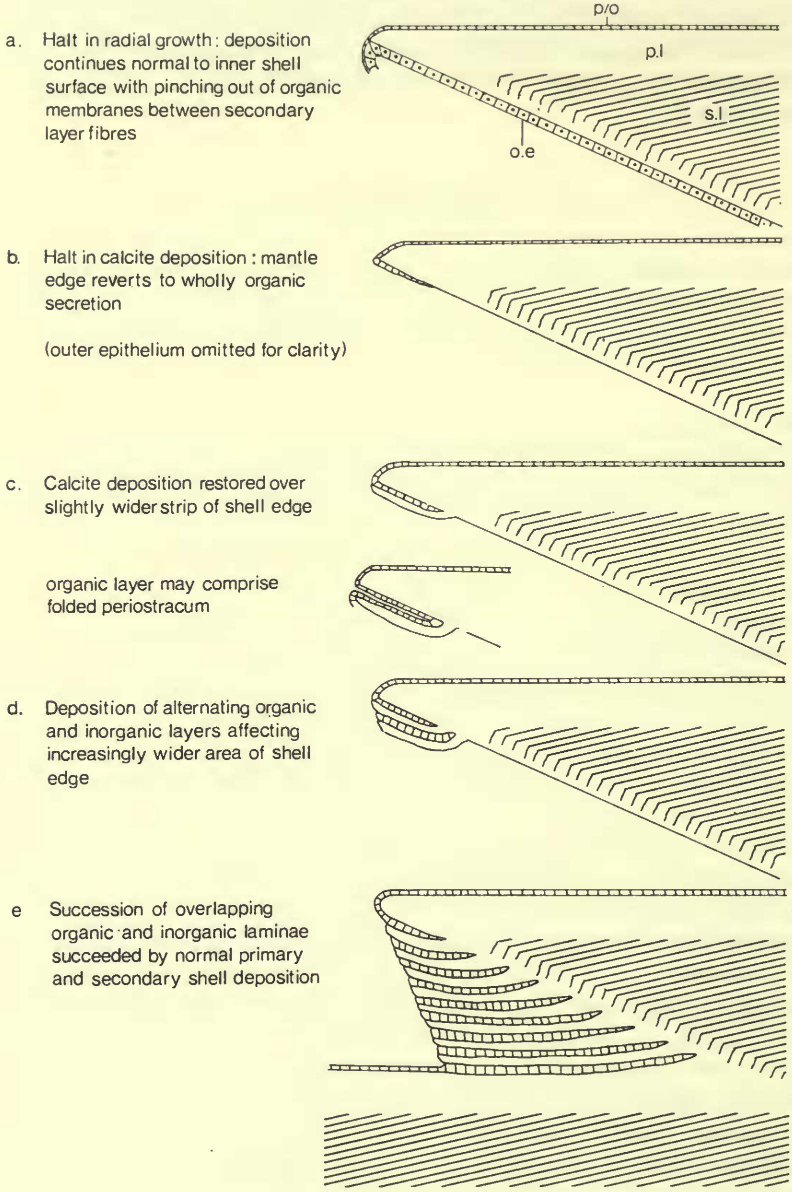
p/o
a. Halt in radial growth: deposition continues normal to inner shell surface with pinching out of organic membranes between secondary layer fibres
p.l
s.l
o.e
b. Halt in calcite deposition: mantle edge reverts to wholly organic secretion
(outer epithelium omitted for clarity)
c. Calcite deposition restored over slightly wider strip of shell edge
organic layer may comprise folded periostracum
d. Deposition of alternating organic and inorganic layers affecting increasingly wider area of shell edge
e Succession of overlapping organic and inorganic laminae succeeded by normal primary and secondary shell deposition

FIG. 4. a–e. Diagrammatic sections to illustrate the formation of a major overlapping shell unit by progressive mantle retractions at a valve margin of *Spiriferina* (p/o – periostracum, p.l – primary layer, s.l – secondary layer, o.e – outer epithelium).

scar are considerably more irregular in outline suggests that the terminal parts of the muscle base, which overlay the associated outer epithelium responsible for secreting myotest, were not evenly distributed. Since the presence of muscles in the vicinity of outer epithelial cells in Recent Brachiopoda has been shown to promote the formation of tonofibrils within each cell body, as well as drastically affecting its secretory behaviour (Williams 1968a : 14), it is reasonable to assume that the outer epithelial cells underlying the muscle bases of *Spiriferina* must have been similarly affected. The linear arrangement of the furrows within the ventral muscle field of *Spiriferina* is consistent with an overlying muscle base which has been segregated into distinct bundles of contractile tissue. Since the furrows, in general, run parallel to the median plane, as do the corrugated grooves on the cardinal process, it is reasonable to assume that the sheet-like bundles of muscle tissue must have run lengthwise in the same direction.

The ventral adductor scars are large in comparison with those of Recent Rhynchonellida and Terebratulida. They are impressed upon both sides of the median septum and consist of a number of furrows which run dorso-ventrally. These furrows are similar to the ones occupying the adjustor and diductor scars and represent the areas of emplacement of the terminal parts of the ventral adductor muscle bases. The median septum is built up of secondary layer fibres, where, in general, the fibres grow from base to apex. Within the dorso-ventrally aligned furrows, however, the shell structure is more irregular and typical of a myotest shell fabric. The contrast between modified and standard secondary layer fibres is well seen in transverse sections through the median septum where the myotest stands out as a zone of small, gnarled, irregularly stacked fibres which lies sandwiched between two layers of more orthodoxly stacked fibres (Pl. 4, figs. 4, 5). The stacking is most unorthodox and there is evidence of fusion of adjacent trails.

Growth of the ventral median septum takes place by the addition of secondary shell material along its anterior facing edge. As the septum expands in size, however, its posterior, earlier-formed parts are gradually overlapped by more secondary shell material deposited subsequently in the umbonal region. This later deposit spreads evenly over the older shell surface and so produces what appears, in transverse section, to be a sharp line of unconformity (Pl. 4, fig. 6).

Around the posterior ends of the ventral adjustor and diductor scars the muscle impressions are very deep. Behind the muscle scars, the shell is considerably thickened by an overlapping accumulation of secondary layer fibres which piled up behind the muscle base. In this area, although some groups of fibres grow anteriorly and antero-laterally, the great majority appear to be directed posteriorly. In radial section, fibres around the posterior part of the muscle scars, showing good cross-sectional outlines, are seen suddenly to change growth directions.

(ii) *Brachial valve*

The quadripartite dorsal adductor scars are situated symmetrically on both sides of a slight median rise, with the anterior pair more closely spaced together than the posterior pair. Viewed at low magnifications, the surface textures of the scars are distinctive and unlike those of the ventral scars. The surface topography of the

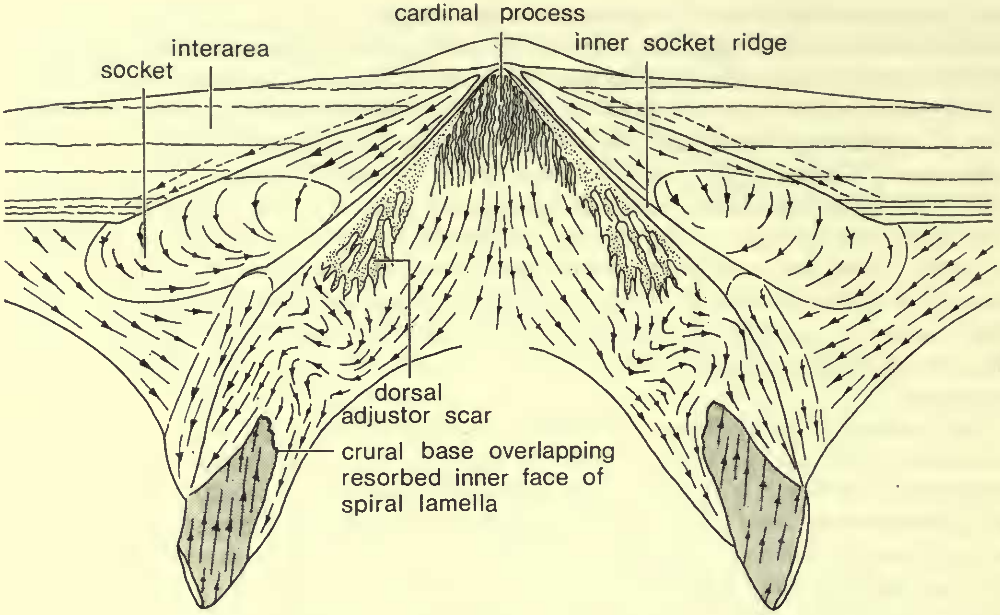

FIG. 5. Stylized drawing of the cardinalia of *Spiriferina* showing the growth vectors of the regular mosaic and the distribution of resorbed (stippled) irregular mosaic.

anterior scars is undulating with puncta occupying hollows between irregularly distributed mounds (Pl. 5, fig. 1). The surface of the posterior scar is, on the other hand, relatively flat. However, both sets of scars appear to be coated with a micritic crust so that the detailed shell ultrastructure cannot readily be discerned. On some parts of the surface, where the sedimentary coating is thin, it would appear that the under-surface is fibrous. However, the skeletal fabric is certainly unusual, for on broken parts of the shell myotest deposits bear little resemblance to the smooth regular outlines of fibres comprising the underlying shell succession (Pl. 5, fig. 2).

The cardinal process and the dorsal adjustor muscle scars are situated close to one another in the umbonal region of the brachial valve (Text-fig. 5). The striate cardinal process of *Spiriferina* closely resembles that of the terebratellacean *Terebratalia transversa* (Sowerby), in that it comprises a series of radially disposed, corrugated ridges, between 50 μm and 100 μm wide, made up of tightly interlocking secondary layer fibres (Pl. 5, fig. 3). The ridges extend from the posterior shell edge to terminate anteriorly as a series of buttresses which rise steeply from the valve floor. Antero-lateral to the cardinal process lie the dorsal adjustor scars which are inserted upon the crural bases. Both the cardinal process and each dorsal adjustor scar are themselves enclosed postero-laterally by an inner socket ridge. The adjustor scars are very deeply impressed upon the shell and, within each scar, a number of narrow stalks composed of secondary shell material project posteriorly at a low angle towards the umbo (Pl. 5, fig. 4). Since the surrounding parts of the shell surface are at a much higher level than that within the scars, it is obvious that the deep impressions of the adjustor scars have been fashioned as a result of strong resorption by the overlying outer epithelial cells which were attached to both dorsal adjustor muscle bases. The narrow stalks protruding from the floor of each scar are therefore not outgrowths of the shell. They are merely remnants of earlier-formed parts of the shell succession which have escaped resorption.

(iii) *Functional considerations*

In examining the surface topographies as well as the shell ultrastructure within the areas of muscle attachment in *Spiriferina*, some attempt has been made to reconstruct the morphology and disposition of its muscle system. The longitudinal 'striation' of the cardinal process and the flabellate pattern of the ventral diductor scars suggest that the diductor muscle fibres were segregated into a number of discrete bundles or sheets whose bases were accommodated within the various depressions of the shell. If the curiously ridged topography of the anterior dorsal adductor scars can be taken as a guide to the nature of the contractile tissue associated with them, then it seems likely that the adductor muscles consisted of a large number of spindle-shaped strands. Each strand was composed of a number of muscle fibres and corresponded to a ridge or hollow on the surface of the scar. However, it is possible that the posterior adductor muscles, like those in a number of Recent articulates (Rudwick 1961 : 1021), were striated. A variation in muscle composition between anterior and posterior adductors might explain the observed differences in surface texture within each pair of scars.

The close proximity of the inner arms of the spiralia and its transverse support, the jugum joining the distal ends of the crura, must have restricted the passage and emplacement of the muscle systems in *Spiriferina* to within relatively narrow limits. However, the size and distribution of the scars points to *Spiriferina* having had a rather strong and efficient muscle system. Mechanically it can be shown that muscles situated closest to the median line are most effective, since it is in such a position that the greatest proportion of the force is used either to open or to close the shell (Armstrong 1968b : 646).

Comparison of the myotest ultrastructures of *Spiriferina* with those of living brachiopods is not easy, for the muscle scar surfaces on which modified mosaic patterns might be displayed are usually badly affected by diagenesis. Either the surface may be covered by a thin micritic layer (as in the dorsal adductor scars) or, when this coating has been removed, the skeletal fabric may appear cracked and pitted (as in the ventral diductor scars). Since terminal faces located well outside the muscle scars of many other fossil genera, as well as *Spiriferina*, are found to be similarly affected, the existence of such ultrastructural irregularities on fibres incorporated within the muscle scars cannot be taken for certain as characteristic of any myotest shell fabric. Even though the detailed morphology of myotest fibres is obscured on the shell surface, some idea as to their overall shape and stacking can be obtained from a study of appropriately sliced radial and transverse sections. On carefully etched surfaces, the myotest fibres can be picked out readily on account of their distinctive size, shape and stacking.

(f) The brachidium

The brachidial apparatus of *Spiriferina* consists of a pair of calcareous spires which extend from the distal ends of the crura and are drawn out laterally away from the median plane. When viewed along the axis of coiling from base to apex, the left-hand spire is coiled clockwise and *vice-versa* for the right-hand spire. Just anterior to the distal ends of the crura, the innermost lamellae of each spire are connected by a curved jugum which is flattened dorso-ventrally (Text-fig. 6).

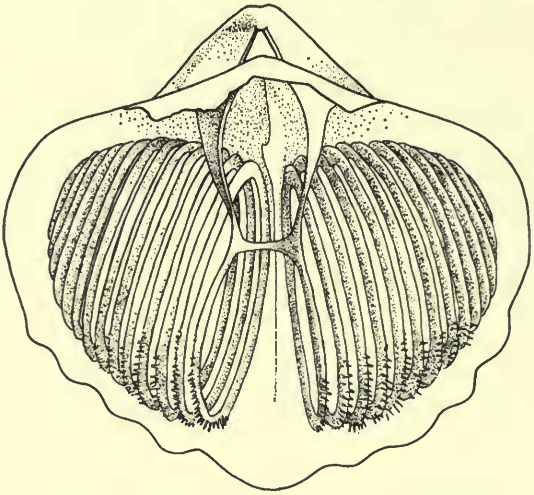

Fig. 6. View of the spiral brachidium of *Spiriferina walcotti* (Sowerby).

Davidson (1852 : 23–24) has given an accurate description of the spires belonging to the closely related species *Spiriferina rostrata* (Schlotheim) which possesses a spiral brachidium virtually identical to that found in *S. walcotti*. In describing the shape of a lamella, Davidson notes that it 'is neither smooth nor of equal thickness on all its width, differing on each side and variable, but always thicker on the inner side of the circumference than on the other which tapers out into an acute edge, and . . . the thickest part of the spire is towards its middle, where it forms a circular elevation, diminishing again towards the outer edge'.

As will be shown, the attitude and outline of the lamellae are important clues to the relationship between lophophore and spiralia. In this study, no set of spires completely free from matrix was available and observations were carried out on carefully selected horizontal and vertical transverse sections of intact spiralia entombed in rock matrix. However, a few fragments were extracted manually, so that it was possible to examine localized parts of the surface mosaic.

The spires are composed of secondary layer fibres which exhibit a distinctive and well-defined pattern of growth. Trails of fibres, exposed on the freshly broken surfaces of fragmentary pieces of spiral lamellae, are found to follow a crescentic path, convex towards the exterior, which runs from the inner to the outer edge of the

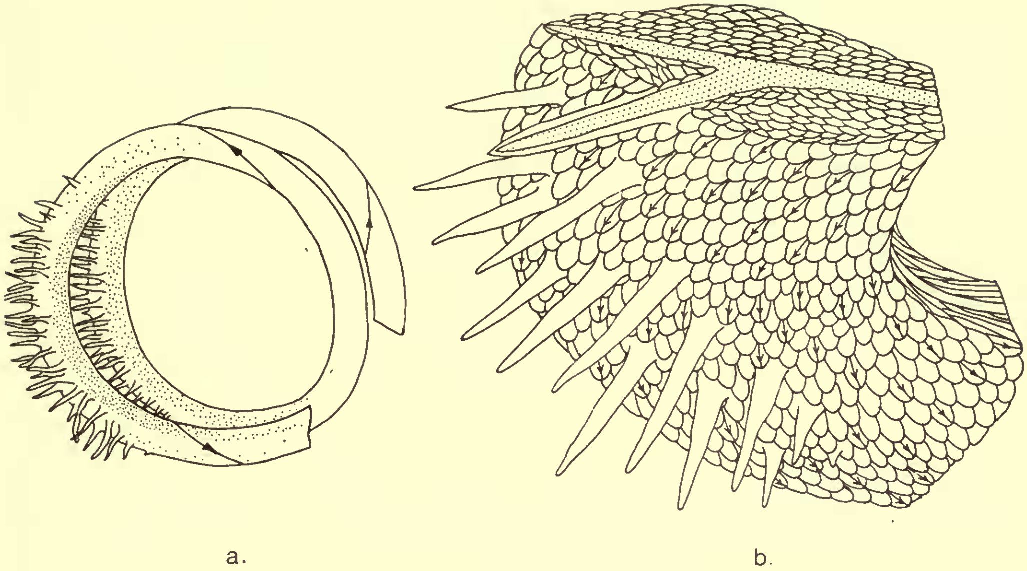

FIG. 7. a. Fragment of a spiral lamella showing the anterior projection of fine spines from the median-facing side. The orientation of fibre trails is shown by growth vectors. b. Schematic diagram of part of a spiral lamella showing the direction of growth of fibres. A mosaic is developed on both sides of the lamella so that, in section, fibres appear to arch outwards in both directions from a median plane. In sections through the innermost whorls, as shown here, a thin layer of non-fibrous calcite (stippled) is interposed between the two sets of fibres and is continuous with spine bases. The blunt inner edge of the lamella is undergoing constant resorption.

lamellae (Text-fig. 7a, b). In *Spiriferina,* shell deposition occurs on both the apical side (facing towards the apex of the spiralium) and basal side (facing towards the base of the spiralium) of the lamellae, so that in transverse cross-sections the convex faces of fibres are seen to arch outwards in both directions from a median plane. In effect, the path followed by each outer epithelial cell responsible for secreting the spiralia appears to be that of an equiangular (or logarithmic) spiral (Text-fig. 8). As the spiralium increases in size, the outer epithelial cells gradually migrate around the lamellae and so contribute to the growth of parts of the spiralium which are progressively more distant from its apex. In addition, if a tangential cut is made on a spiral lamella, the observed overlapping disposition of the long axes of secondary layer fibres (Text-fig. 9) indicates that, for the spiral lamella to expand continuously to fill the brachial cavity, new cells (and hence new fibres) must be proliferated continuously in a linear generative zone along the sharp leading edge of the lamella.

On certain parts of the spiralia there are surfaces of resorption. An area of resorption is readily recognized by the absence of a surface mosaic which is usually replaced by long exposed trails of fibres possessing no recognizable terminal faces. In transverse cross section, provided the surface of resorption is not coplanar with a growth surface, the distinction is clear-cut. The distinctive mode of stacking of fibres provides a convenient 'way-up criterion' (Williams 1968a : 8). The profile of the keel, which is convex towards the growing surface, serves to indicate the precise attitude of the depositional surface in that part of the shell at that moment in time. If groups of fibres, stacked in rows one above the other, are truncated by the existing surface profile, then resorption must have taken place.

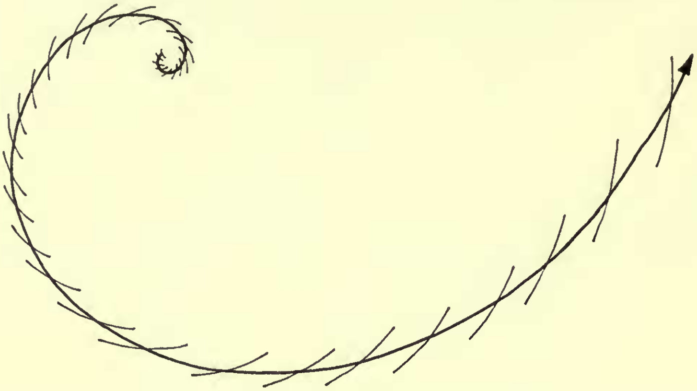

FIG. 8. Reconstruction of the growth path of a single fibre contributing to the growth of a spiral lamella. Only a small segment of the spiral is present at any one time since the inner edge of a lamella is constantly being resorbed.

Around the blunt inner edges of the lamellae fibres are resorbed. Some resorption also occurs on the basal sides of lamellae, especially on the posterior facing halves of the spires. Towards the dorsal and ventral extremities of each lamella, the zone of resorption gradually decreases until practically all outer epithelial cells on the basal side are actively secreting. As previously mentioned, the outer epithelial cells responsible for secreting each spiralium continually migrate backwards along the curved lamellae towards the median plane. This process does not continue indefinitely, however, for on the dorsal surface of the innermost lamellae of both spiralia, lateral to the jugum, resorption takes place.

On the anterior facing parts of the lamellae a considerable number of small spines project outwards at an oblique angle (Text-fig. 7a, b). As a rule, the spines always project from the basal sides of the lamellae whilst on the apical side the surface is devoid of any unusual outgrowths. Structurally they resemble the calcareous rods (taleolae) which permeate the shells of Plectambonitacea such as *Sowerbyella* (Williams 1970 : 339), in that the secondary layer fibres, deflected around the obliquely inclined cylindroid bodies, arch outwards towards their distal extremities. If the anterior facing part of a spiral lamella which bears the spinose projections is sectioned horizontally, the mode of formation of the spines becomes apparent from an examination of the newly exposed shell succession. Such sections of the innermost whorls of the spiralia expose a thin layer of non-fibrous calcite, about 10 μm wide, which runs from the blunt inner edge to the sharp outer edge of each lamella

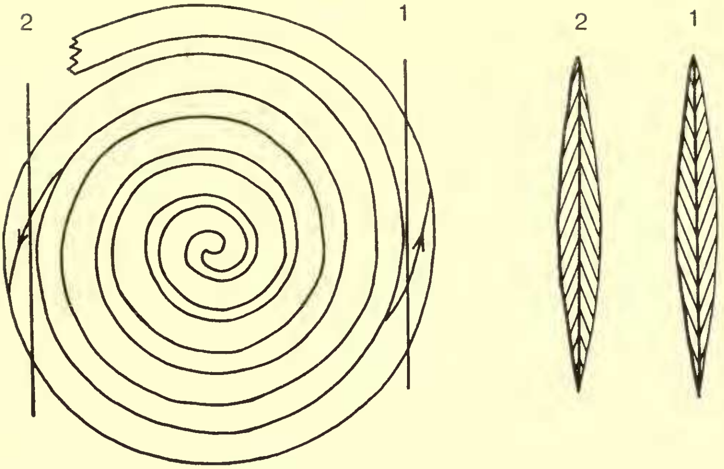

FIG. 9. Lateral view of a spire of *Spiriferina* showing lines of tangential section and the growth direction of fibres. In the anterior section (1), fibres diverge upwards from a median plane whereas in the posterior section (2), the fibres diverge downwards.

(Text-fig. 7b). At infrequent intervals, cylindroid bodies up to 60 μm in diameter swell out from this layer (on only the basal side of the lamella) and cause the surrounding secondary layer fibres to be deflected around them on all sides. Judging from the morphological differences between spines and fibres, and the sharpness of boundaries between them, there is every indication that each was deposited by a different type of cell. The manner in which the bases of spines are submerged in secondary layer fibres points to each spine having first been secreted by a small tubular evagination of specialized epithelium situated around the sharp, outer edge of the spiral lamella. As the diameter of each spiral whorl increased, the bases of spines were gradually overlapped by successive secondary layer fibres until finally they became engulfed in the resorbing epithelium situated at the blunt inner edge of the lamella. As well as forming the cores of the innermost whorls of the spiralia, the homogeneous calcite layer is also present within the jugum where it forms a prominent inner layer in transverse section. On the outer whorls of the spiralia, however, the layer is no longer present but spine bases continue to disrupt the shell succession. Evidently the specialized epithelium which gave rise to the subsidiary layer occupied the outer edges of the innermost spiralia and the jugum, but on the outer whorls was concentrated only in small circumgenerative zones which gave rise to isolated spinose outgrowths that did not otherwise affect the shell succession. The fact that the spines are situated only on that part of the spiralia facing the commissure tends to suggest that they may have served some protective function. The spines may have acted either as a prickly deterrent to predators seeking to devour the soft parts of the animal, or as a grille preventing coarse particles of sediment from entering the brachial cavity (assuming a lophophore current system which filtered food and water inwards through the arms of the spiralia).

(g) Articulation

The articulation provided by the teeth and sockets of *Spiriferina* is highly effective. Each is composed of secondary layer fibres, and by plotting the long axes of exposed trails as growth vectors, growth maps can be constructed for both structures. Since each fibre is a record of the path taken by each corresponding outer epithelial cell, growth maps can be used to interpret the nature of the build-up of both exoskeletal outgrowths in terms of bulk epithelial movements.

The dental sockets extend along the inner margins of the notothyrium from the umbo to the hingeline. On the median-facing side, each socket is bounded by a stout inner socket ridge whilst the overhanging edge of the interarea functions as an outer socket ridge (Text-fig. 5). Each socket can be divided into two regions with the anterior part forming a much deeper depression than the posterior part. In the anterior part, which accomodates the distal end of the tooth, the fibres grew across the socket from the overhanging edge of the interarea towards the inner socket ridge. In the posterior part, which was no longer involved in articulation and does not now come into contact with the point of the tooth, the fibres grew along the floor of the socket from the umbo outwards. As the outer surface of the dorsal interarea is composed of primary shell material, the directions of growth of the underlying secondary layer fibres are normally obscured. However, in specimens where the primary layer has been removed, the secondary layer fibres are seen to be directed outwards from the umbo parallel to the edge of the notothyrium.

The teeth and dental plates stand out as prominent features in the umbonal region of the pedicle valve. As well as functioning as part of the hinge mechanism, lateral outgrowths of the teeth also serve to restrict partially the triangular delthyrial opening. What appear, at first sight, to be a pair of disjunct deltidial plates are structures composed solely of secondary shell material. Each structure arises from that part of the tooth bordering the delthyrium and is fashioned into a laterally projecting ridge which runs from the apex of the delthyrium to the hinge line (Text-fig. 10). As similar ridged outgrowths of the teeth have been found bordering the delthyrium of *Spirifer trigonalis* (Dunlop 1962 : 491) and given the name *dental ridges*, it seems reasonable to apply the same terminology to the corresponding ridges in *Spiriferina*. The fibres comprising each dental ridge in *Spiriferina* grew along the length of the ridge from the delthyrial apex to the hinge line. Over the greater part of each tooth, fibres grew towards the distal end. However, on the side facing into the delthyrial cavity the pattern is more complex.

From the hinge line, part of the shell swells into a large bulbous ridge which is situated on the median-facing side of the tooth and just inside the dental ridge (Pl. 6, fig. 1 ; Text-fig. 10). This unusual outgrowth, which has been observed in every specimen so far examined, cannot be involved in articulation as it is situated on the opposite side of the hinge line from the distal end of the tooth. At its widest part the ridge is flattened and appears abraded. This observation is confirmed by a closer inspection of the surface which shows the exposed parts of fibres comprising that part of the ridge to be ragged and misshapen (Pl. 6, fig. 2). Due to the absence of any exoskeletal outgrowths on the brachial valve in the immediate vicinity, which

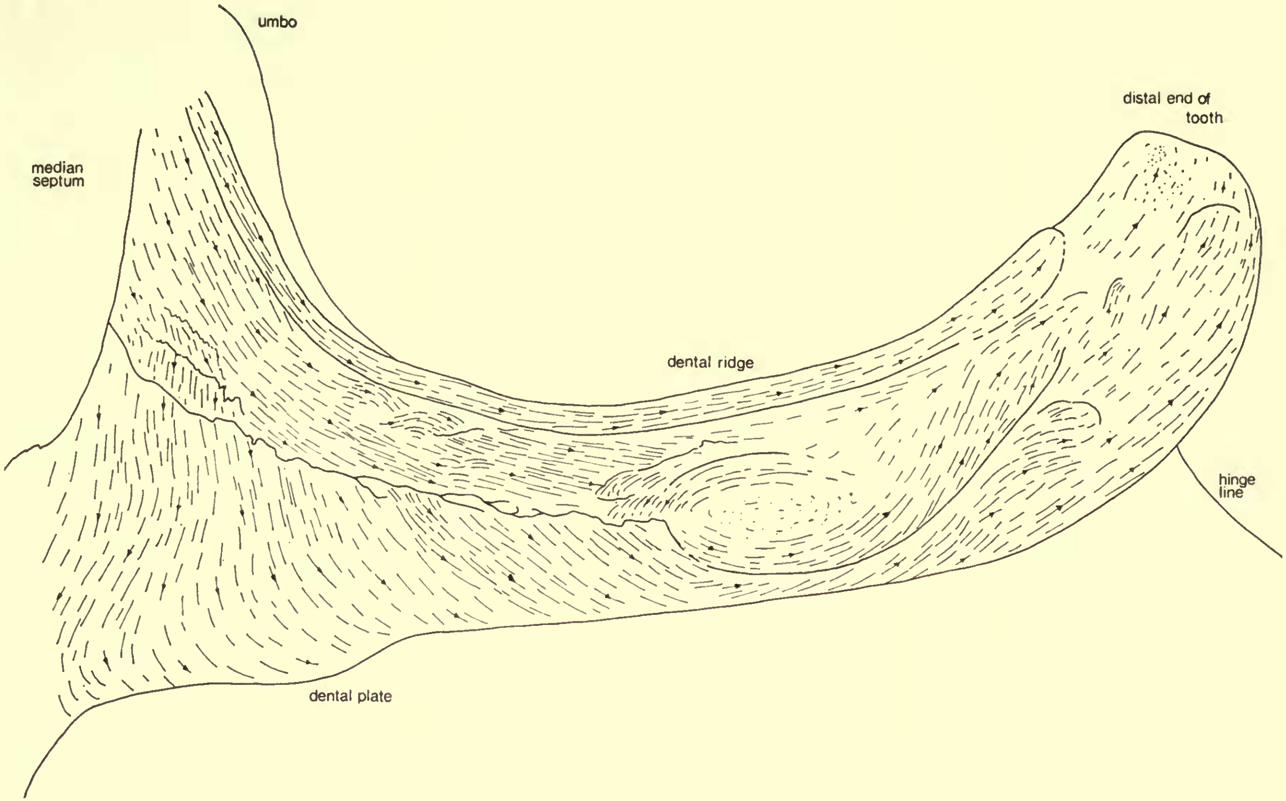

FIG. 10. Sketch of a tooth and associated structures of *Spiriferina* showing growth vectors of the secondary shell mosaic.

as a result of rubbing against the ridge could have given rise to such a shell fabric, it seems likely that the abrasion must have been caused by pressure and possible movement around the proximal end of the pedicle.

Both teeth fit snugly into the sockets of the brachial valve, but despite having to grow in a partially confined space, the distal extremities are still the main areas of growth on the teeth. In radial section, the cross-sectional outlines of fibres comprising the distal ends of the teeth show a rhythmic variation in direction of growth (Pl. 6, figs. 3, 4). At the point of the tooth the epithelium appeared to move in four consecutive directions – dorsally, laterally, ventrally, laterally – and then the sequence is repeated. If the two lateral movements of the cycle were in opposing directions, as seems likely, then the motion would be helical.

IV. SHELL STRUCTURE OF OTHER SPIRIFERIDA

(a) Atrypidina

According to Boucot *et al.* (1965 : H632), the Atrypidina are divided into two superfamilies based on the attitude of the spiralia. The Atrypacea bear spiralia with apices directed medially or dorso-medially, whereas the spiralia of the Dayiacea are directed laterally or ventrally. From an evolutionary standpoint, the Atrypidina are important since they include the earliest forms of spire-bearing brachiopods. Cooper (1956 : 136) cites a small undescribed form from the Row Park Formation of Maryland and another, possibly the same species, from the Crown Point Formation of New York (both Middle Ordovician) as stratigraphically the oldest yet recorded, but interior details of neither are known. They both appear to have '*Protozyga*-like' shells, and on this basis Cooper regards the slightly younger *Protozyga* s.s. as the most primitive of all Spiriferida. By late Ordovician times several stocks of spire-bearing brachiopods had become established. These include the small costate or multiplicate atrypaceans *Protozyga*, *Zygospira*, *Hallina* and *Catazyga*.

(i) *Atrypacea*

Though impunctate, the calcareous shell succession of *Protozyga elongata* Cooper from the Lower Bromide Formation (Upper Ordovician) of Oklahoma is broadly comparable with that of *Spiriferina walcotti* (Sowerby). *P. elongata* is small, seldom more than 5 mm in length, and thin-shelled. Its primary layer, measuring up to 10 μm in thickness, is composed of narrow crystallites with long axes disposed normal to the isotopic primary/secondary layer boundary. The secondary layer is also comparatively thin and has not been found to exceed 50 μm. Transverse sections across the widest part of the shell reveal a succession of small, flattened fibres which although irregular in profile are stacked in a very compact fashion (Pl. 6, fig. 5). Close to the valve margins fibres measure between 4 μm and 6 μm in width, but towards the postero-median regions of the same specimen lateral boundaries of individual fibres tend to amalgamate and produce a more massive skeletal fabric. In view of the irregular nature of the remainder of the skeletal succession, which may in any case have been diagenetically induced, it would be hazardous to guess as to the physiological significance of such a variation in fabric. However, if the overall irregularity in fibre profile is a primary feature, then the welding together of adjacent parts of fibres may reflect deposition by outer epithelial cells whose normal secretory processes were disrupted due to the encroachment of a muscle base. Were it not that *Protozyga* possessed a rudimentary spiralium of generally less than one convolution, it might easily be mistaken for a small, mildly plicate rhynchonellid.

Compared with *Protozyga*, *Zygospira* is further advanced along the spiriferid line of descent, in that it possesses a more fully developed spiralium of up to four convolutions with apices directed medially. Specimens of *Zygospira modesta* (Say), collected from beds assigned to the Richmond Group (Upper Ordovician) exposed near Nashville, Tennessee, reveal a secondary shell fabric which is more regular than that of *Protozyga elongata*. Although the shell exterior of *Zygospira* is markedly costate, the undulations of the costae are not preserved on the inner surface of the valves. When traced any great distance from the shell margins, the secondary layer fibres tend to fill out and eliminate the undulations so that both valves are thickened below the ribs and correspondingly reduced below the intervening grooves. Cross-sectional outlines of mature secondary layer fibres generally conform to a flattened diamond shape and measure about 10 μm to 12 μm in width (Pl. 6, fig. 6). As shown below, the outlines of sectioned secondary fibres are important in providing a means of deducing the pattern of the internal secondary shell mosaic. On this basis, the terminal faces of *Zygospira* are clearly rhomb-shaped (as opposed to smoothly curved in *Spiriferina*) with the longer diagonal of each rhombohedron coincident with the long axis of each corresponding fibre trail. The regular diamond-shaped outlines of fibres, though present over the greater part of both valves, are disrupted within the vicinity of the dorsal and ventral muscle scars ; but such localized modifications in the secretory regime do not lead to any great thickening of the shell succession in either valve.

In the related *Catazyga headi* Billings from the Richmond Group of Adana County, near Winchester, Ohio, the pedicle valve in particular is greatly thickened around its posterior regions. Anteriorly the shell thickening is confined to a median platform, probably a muscle platform, but towards the umbonal region deposition becomes more pronounced in the areas laterally adjacent to the scars. As a result of this postero-lateral shift in the main zone of calcification the level of the ventral muscle scar surface changes from being an area which anteriorly was above that of the surrounding floor to that of a deep impression. In cross-section, a primary layer about 20 μm thick is succeeded by secondary layer fibres which are diamond-shaped, like those of *Zygospira* (Pl. 7, fig. 1). Fibres comprising the lateral and anterior regions of both valves usually measure between 10 μm and 12 μm in width, but away from the margins there is an increase in fibre size with widths of 20 μm to 25 μm becoming common. Within the areas of maximum shell deposition, the secondary fibres give way to a coarse tertiary prismatic layer (Pl. 7, fig. 2). Compared with the uniformly stacked 'columns' of the Recent terebratulide *Gryphus vitreus* (Born) (MacKinnon 1971b : 41), the tertiary layer of *Catazyga* is rather irregular. This is due mainly to the impersistent nature of adjacent crystal boundaries which, though generally aligned normal to the inner shell surface in true 'prismatic' fashion, tend to migrate laterally from time to time. The whole of the tertiary layer appears to take on a 'jigsaw-puzzle' type of shell fabric which is considered to be transitional between that of an orthodoxly stacked secondary layer and the more conventional 'columnar' tertiary layering which is typical of certain later spiriferide genera. In places, the prismatic shell material gives way both laterally and vertically to normal fibrous outlines, so that the outer epithelial cells responsible for secreting the tertiary layer were obviously capable of reverting to secondary shell deposition. The probability is high that such a distinctive tertiary layer fabric is original, for gently etched sections of *Catazyga* are, in places, traversed by a fine depositional banding. The banding, which persists across numerous adjacent crystalline boundaries, is similar to that found in sections of living *Gryphus*.

Around the shell margins of *Catazyga* there is evidence that the mantle became detached periodically or, at least, reverted to primary shell deposition. From a point near the outer shell edge, a wedge of primary shell material, about 35 μm at maximum thickness, dips posteriorly inwards to terminate a short distance from the inner shell surface (Pl. 7, fig. 3). This wedge is bounded on either side by orthodoxly stacked secondary layer fibres. Unlike similar wedges occurring in some Recent Brachiopoda, the primary shell material is not massive but is composed of a series of regularly stacked crystallites between 8 μm and 12 μm in width which stand at right angles to the earlier-formed parts of the secondary shell succession. As the boundaries between primary and secondary deposits are indistinct, it is not known for certain whether a clear break in deposition did occur before the changeover. However, if the fabric of the primary shell wedge is original, it is possible that organic membranes, continuous with those in the preceding secondary layer, ensheathed the primary layer crystallites. For such to be the case would not require complete mantle detachment, but merely a temporary reversal from secondary to primary shell deposition.

Contemporaneous with the ribbed zygospirid stock, but less common, are certain smooth-shelled Atrypacea, including *Idiospira*, which are assigned to the family Lissatrypidae. In transverse sections of *Idiospira thomsoni* (Davidson), from the Craighead Limestones (Caradoc) of the Girvan district, the outlines of secondary layer fibres are variable. Some sections show neatly stacked fibres with smooth curved outlines (Pl. 7, fig. 4), which contrast with the sharp, angular outlines of fibres comprising the shells of *Zygospira* and *Catazyga*, whereas other parts of the shell succession (Pl. 7, fig. 5), exhibit irregular outlines which resemble those of *Protozyga*. Judging from the way in which, in *Idiospira*, these fibres with smooth symmetrical outlines are seen to merge with neighbouring groups of irregularly stacked fibres, it seems highly likely that the latter are the product of secondary recrystallization across adjacent fibre boundaries. If this is the case, then the original secondary shell mosaic of *Idiospira* consisted of alternating rows of smooth spatulate terminal faces and not diamond-shaped outlines as in other Atrypacea. No tertiary layer has been found in *Idiospira*.

In Silurian and Devonian Atrypacea the external (and internal) morphology of both valves became highly diverse, yet much of this variety of form can be rationalized into two main components. These are a radial pattern of ribs and a concentric pattern of overlapping growth lamellae (Copper 1967 : 123) ; both components are usually built up from primary and secondary shell material. Complete specimens of five Siluro-Devonian forms were available for study. These were *Atrypa reticularis* (Linné) from the Wenlock Limestone of Shropshire, *Atrypa* sp. from the Upper Hamilton Group (Middle Devonian) of New York, *Atrypina hami* Amsden from the Haragan Formation (Lower Devonian) at White Mound, Murray County, Oklahoma, *Spinatrypa* sp. from the Hackberry Stage (Upper Devonian) of Rockford, Iowa, and *Desquamatia subzonata* Biernat from the Givetian shales of Skaly in the Holy Cross Mountains, Poland.

In all five stocks, the primary layer is well developed and usually attains a maximum thickness of up to 40 μm below the rims of overlapping growth lamellae where it is best protected from abrasion. As well as revealing a porous texture, sections of this thin outer layer (e.g. Pl. 7, fig. 6) show it to be traversed by a fine lineation which is orientated either at a steep inclination or normal to the outer shell surface.

The shape and stacking of secondary layer fibres are also remarkably uniform and compare well with those of *Catazyga* and *Zygospira* (but not *Idiospira*). In sections of the Middle Devonian species of *Atrypa* the outlines of secondary layer fibres are well defined (Pl. 8, fig. 1). Diamond-shaped profiles of sectioned fibres which measure, on average, about 25 μm in width are characteristic not only of this genus but also of all other representatives examined. Since even the early zygospirid stocks exhibit similar fibre outlines, it seems reasonable to assume that this feature was common to the family Atrypidae as a whole. In this respect, representatives of the Lissatrypidae (the smooth-shelled Atrypacea) have still to be investigated.

Copper (1967 : 127) has examined optically the shell structure of a number of Devonian Atrypacea by means of cellulose acetate peels. In more 'advanced' and 'complex' atrypids like *Gruenewaldtia*, *Mimatrypa*, *Spinatrypa* and *Atryparia*, he reports that secondary layer fibres are consistently larger than those of other related genera.

At regular intervals in the shell succession, groups of secondary layer fibres are outwardly deflected towards the primary layer in a manner reminiscent of punctation, but at the centre of such deflections no hollow canals are found. Instead, the clear-cut diamond-shaped outlines of fibres degenerate into a central nucleus of irregularly interwoven accretions (Pl. 8, fig. 2) which resemble in appearance the myotest shell fabric of certain living articulates, such as *Notosaria*. Since the outer epithelial cells responsible for the deposition of the latter are known to be permeated by dense concentrations of tonofibrils associated with muscle attachment, it is reasonable to assume that the cells responsible for the outward deflections of the *Atrypa* shell must have been affected to a similar degree. Over the greater part of the inner shell surface, excluding muscle areas and exoskeletal outgrowths, these outward deflections of the secondary layer find expression as a series of pits which have been recognized, in the past, as gonadal markings (Pl. 8, fig. 3). Presumably the gonads were attached to the outer epithelium and caused it to bulge outwards at points represented by the pitting on the shell surface. Modifications in the shell surface can thus be attributed to a breakdown in the normal processes of deposition such as are found under muscle attachment areas with a localized spread in the organic secretory phase and a corresponding reduction in mineral exudation.

The concentric overlapping growth lamellae adorning the surfaces of so many Atrypacea were deposited by the marginal parts of both mantle lobes, which were subject to periodic fluctuations in secretory behaviour (Pl. 8, figs. 4, 5). Both primary and secondary shell layers are affected but not in the manner described for *Spiriferina.* The structural relationships between overlapping shell units are, however, closely comparable with those described for Recent articulates by Brunton (1969 : 192) and Williams (1971a : 61). Each planar surface, along which the normal sequence of shell deposition was interrupted, dips posteriorly at a low angle towards the shell interior. In all genera examined, such regression planes invariably interrupt the secondary shell succession and none was found which could be considered to have affected only the primary layer. Sandwiched between the regression plane and the immediately younger parts of the shell succession is a wedge of primary shell material which thins posteriorly. Where the wedge thins out, the regression plane is marked by a narrow zone of sharply flexed fibres which can be traced running posteriorly for a short distance before becoming lost in the remainder of the secondary shell succession.

In the coarsely plicate form *Spinatrypa,* tubular prolongations of the ribs extend outwards from the inner edge of each prominent overlapping growth lamella. The spines grew in such a way that their development was complete before the onset of the succeeding mantle regression. Initially a spine was merely a gently curved extension of a rib-crest but gradually, due to peripheral accretion, the opposing edges grew round towards one another and met on the underside (Text-fig. 11). Where the two edges have come together a seam is preserved. The spines are built up from primary and secondary shell material.

Since each concentric row of spines is succeeded by a plane of regression, it is evident that no sooner had a row of spines grown to maturity than its outer epithelial lining became detached due to mantle retraction. If the regression was slow, the inner surfaces of spines may have been covered by a periostracal deposit, but in any case they could not have been functional for any length of time. With the onset of shell deposition after the mantle regression the base of the spine was overlapped by subsequent primary and secondary shell layers so that no further contact with the mantle was possible.

In addition to possessing a well-developed primary and secondary shell succession, Silurian and Devonian Atrypidae are characterized by an inner tertiary layer deposit which may be massive or interdigitate with parts of the secondary layer (Pl. 8, fig. 6). The tertiary layer attains maximum thickness in the postero-median region of both valves, but around the valve margins only primary and secondary shell deposition occurs. The nature of the tertiary layer is variable, even within a single specimen, and may either consist of a series of vertically disposed crystals with well-defined boundaries or be massive. When clear-cut crystal boundaries are present they are commonly in structural continuity with the outlines of underlying secondary layer fibres.

Tertiary layer deposits are also found within muscle scars. In *Atrypa,* the areas of muscle attachment are deeply impressed on the inner surfaces of both valves. In

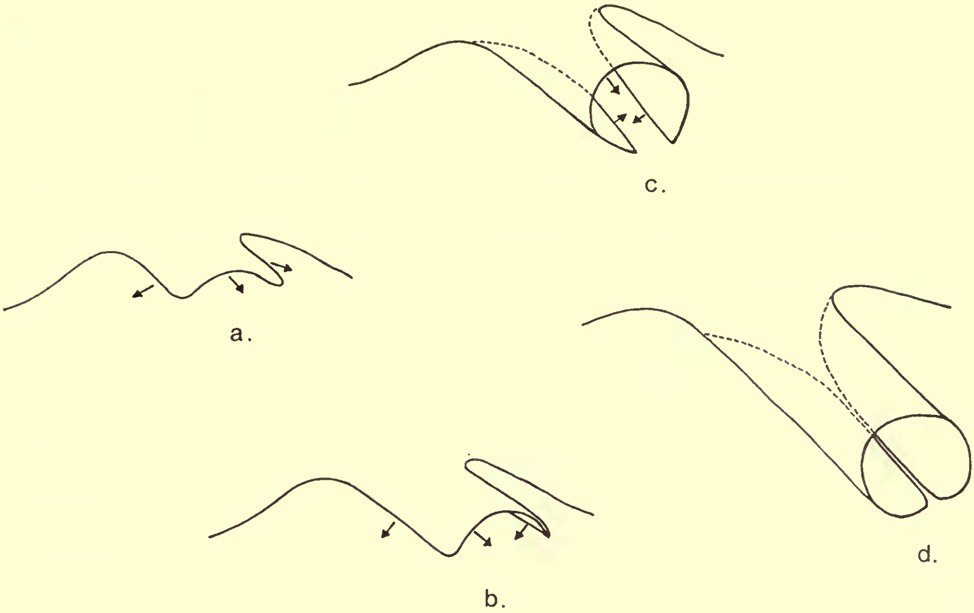

FIG. 11. a–d. Progressive stages in the formation of a tubular spine at the anterior edge of an overlapping growth lamella in *Spinatrypa*. Opposing edges grow round towards one another (see arrows) to meet on the underside.

transverse sections through the ventral muscle scars, a succession of secondary and tertiary layers in alternation is unconformably overstepped by a thick tertiary prismatic myotest (Text-fig. 12). The junction between myotest and underlying shell layers is sharp (Pl. 9, fig. 1) and, judging from the way in which successive secondary and tertiary layers are overlapped, it is evident that earlier-formed parts of the shell succession which lay in the path of the advancing muscle base were resorbed. An examination of ultrasonically cleaned ventral adductor and diductor muscle scar surfaces reveals a fabric very similar to that found in *Gryphus*. The outlines of individual crystals are highly irregular and lateral margins of adjacent ones interdigitate (Pl. 9, fig. 2). These terminal faces of tertiary layer crystals, upon which deposition took place, are rough and undulating and although some of this unevenness may be due to secondary diagenetic effects, it is probably for the most part original. Outside the muscle scars the terminal faces of tertiary layer crystals are virtually the same as those inside, and no clear-cut distinction between them at the submicroscopic level can be made.

Deposition of the atrypid tertiary layer must have taken place in a manner very similar to that occurring in living *Gryphus*. Instead of depositing obliquely disposed fibres ensheathed by protein membranes, the tertiary layer epithelium reverted to deposition in a plane normal to the inner shell surface. As Copper has shown (1967 : 129), there are some differences in the size and distribution of the secondary and tertiary layers within the atrypid group as a whole. Both *Atrypa* and *Desquamatia* examined by 'Stereoscan' show generous interlayering, but in later *Desquamatia*, according to Copper, the interlayering decreases. The disappearance of numerous interlayers and the thickening of the tertiary layer are also typical of *Spinatrypa, Spinatrypina, Atryparia* and *Kerpina*. In *Gruenewaldtia* and *Mimatrypa* the tertiary layer thickening becomes extreme and adjacent crystals merge to produce a more massive deposit.

(ii) *Dayiacea*

The Dayiacea include both smooth and plicate forms which bear spiralia with laterally or ventrally directed apices. In the earliest known genus *Cyclospira*, however, the spiral lamellae are coiled more or less in a plane parallel to the median plane of the valves. Although *Cyclospira* is reported to be ajugate, it closely resembles *Dayia* in morphology. Both have smooth, unequally biconvex shells with their pedicle valves more convex, and Schuchert and Cooper (1932 : 27) drew attention to the close similarity in their ventral muscle scars. The only other representative of the Dayiacea examined was *Coelospira*, which differs from the other two mainly in being plicate.

Although much of the shell material of *Cyclospira* sp. from the Upper Ordovician (Ashgillian) of Pomeroy, Co. Tyrone, Northern Ireland, was altered by recrystallization, it was possible to recognize parts of the secondary and tertiary succession. No primary layer was preserved. Secondary layer fibres which are diamond-shaped in transverse section measure about 12 μm in width (Pl. 9, fig. 3). The best preserved parts of the tertiary shell succession were located below parts of the ventral muscle scars. In those areas, the boundaries between tertiary layer crystals are impersistent but a prominent depositional banding delineates former cell boundaries (Pl. 9, fig. 4). The thickness of individual growth increments varied between 0·2 μm and 0·8 μm and prominent bands could be traced running across several adjacent crystal boundaries. The banding is closely comparable with that observed in sections of the tertiary layer of *Gryphus*.

A specimen of *Dayia navicula* (Sowerby) from the Dayia Shales (Ludlovian) of Shropshire provided the history of exoskeletal secretion in that genus. Both valves had been largely stripped of their thin outer primary layer but secondary layer fibres up to 20 μm wide showed good diamond-shaped outlines in transverse section (Pl. 9, fig. 5). As far as is known, tertiary layer deposits (Pl. 9, fig. 6) are restricted to the posterior regions of the pedicle valve, for no such deposit has been found in the brachial valve. The median septum which adds thickness to the brachial valve is composed solely of secondary shell material. Vertically stacked tertiary layer crystals have clearly defined outlines which measure, on average, 18 μm in thickness. These outlines are initially in continuity with the outlines of underlying secondary layer fibres. The overall pattern of tertiary layer deposition resembles that of *Catazyga* in that individual crystals are laterally deflected either one way or the other at fairly regular intervals to produce a 'jigsaw-puzzle' type of shell fabric. No interlayering of secondary and tertiary layer deposits was noted.

Although the only specimen of *Coelospira* available for study (*Coelospira saffordi* (Foerste) from the Brownsport Formation of Western Tennessee) was found to be

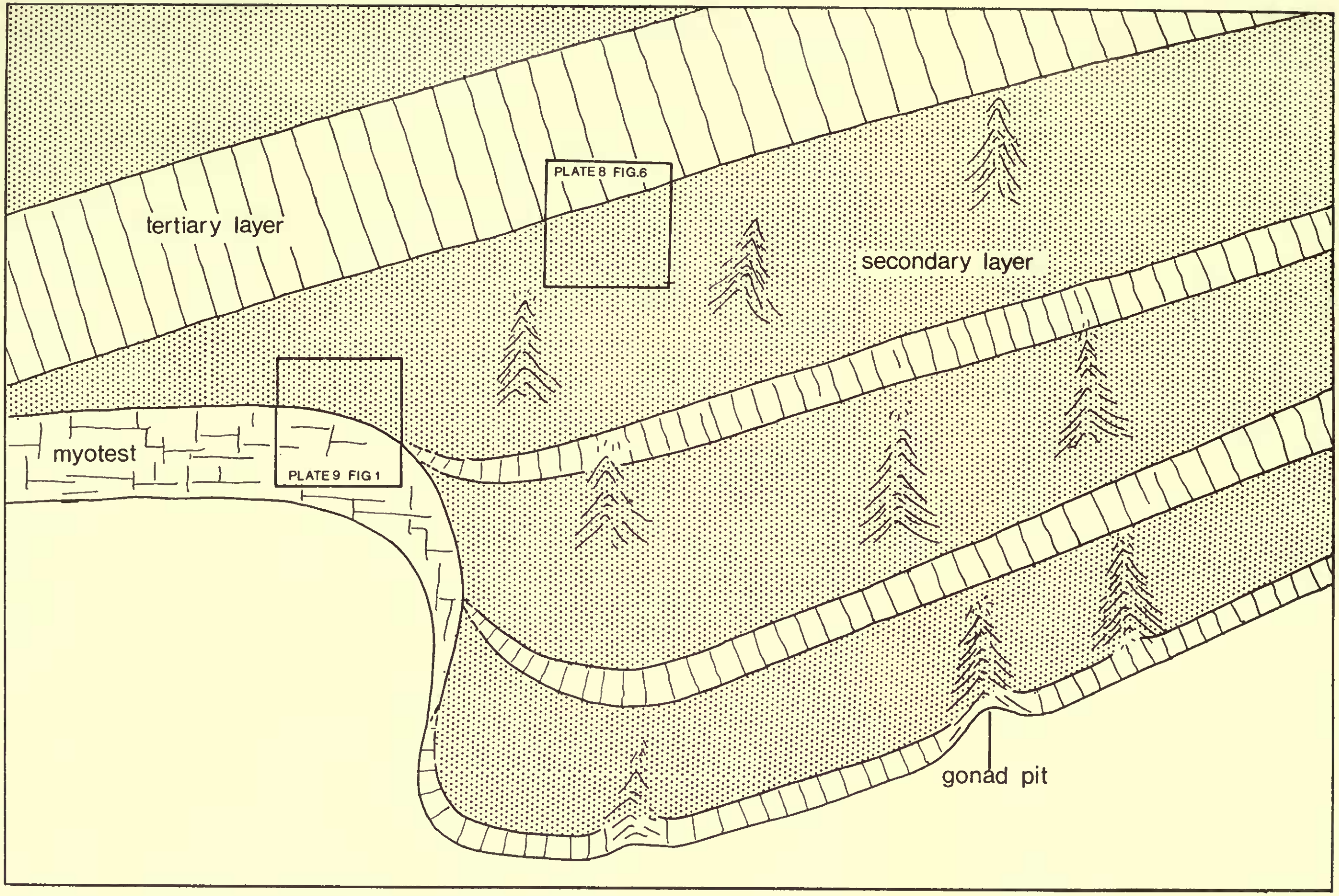

Fig. 12. Stylized section through part of a pedicle valve of *Atrypa* showing the distribution of secondary and tertiary layers. The ventral myotest is situated at a lower level than the surrounding floor of the valve and 'oversteps' earlier-formed parts of the shell succession. The locations of Plate 8, fig. 6 and Plate 9, fig. 1 are shown.

partially silicified, remnants of three calcareous shell layers were recognized. The primary layer, which attains a thickness of about 12 μm, is composed of narrow crystallites stacked normal to the outer shell surface. The outlines of secondary layer fibres tend to be more rounded than those of other Dayiacea or Atrypacea, apart from *Idiospira*, and cross-sections reveal orthodoxly stacked groups with gently curved keels and saddles (Pl. 10, fig. 1). Shell deposition in the postero-median region of the pedicle valve was about three times as great as that in the corresponding part of the brachial valve. A thick tertiary layer, which has no counterpart in the brachial valve, augments the pedicle valve succession (Pl. 10, fig. 2). As in *Catazyga*, secondary layer fibres comprising the flanks of the pedicle valve pass laterally into a more massive tertiary layer which coincides roughly with the areas of ventral muscle attachment. The fabric of the tertiary layer in *Coelospira* is similar to that found in *Dayia*.

(b) Retziidina

The suborder Retziidina comprises costate and multiplicate rhynchonelliform Spiriferida with a medially directed V-shaped jugum and laterally directed spiralia. On the basis of presence or absence of shell punctation, the suborder is split into two superfamilies, respectively the Retziacea and Athyrisinacea (Boucot *et al.* 1964 : 813). Specimens of only four punctate genera were available for study. These were *Homeospira evax* (Hall) from the Waldron Formation (Upper Silurian) of Indiana, *Rhynchospirina maxwelli* Amsden from beds of the Haragan Formation (Lower Devonian) at White Mound, Murray County, Oklahoma, *Hustedia radialis* (Phillips) from the Arden Limestone (Lower Carboniferous), Arden, Lanarkshire, and *Retzia* sp. from the St Cassian Beds (Triassic) of Northern Italy.

A well-developed primary layer, on average 25 μm thick, is characteristic of all four genera. In the *Rhynchospirina* (Pl. 10, fig. 3) and *Homeospira* (Pl. 10, fig. 4) it was found to be partially recrystallized, but in *Hustedia* (Pl. 10, fig. 5) and especially *Retzia* (Pl. 10, fig. 6) features such as the porous texture and fine lineations disposed normal to the shell layers were seen, reminiscent of the primary layer fabric of Recent articulates. In *Retzia* sp. a fine depositional banding with an average periodicity of 0·8 μm has been recognized (Pl. 11, fig. 1). This banding, which is considered to be diurnal, dips posteriorly at a low angle from the outer shell surface to the inner primary/secondary shell layer interface.

Fibres comprising the secondary layer of the Retziidina are consistently small. Indeed, in none of the genera examined were any found which had grown to a width much in excess of 10 μm. Secondary layer fibres of *Homeospira* and *Rhynchospirina* are generally rather irregular in outline although this unevenness is probably of secondary diagenetic origin. However, in *Retzia* and *Hustedia* transverse sections reveal orthodoxly stacked fibres which possess smoothly rounded keels and saddles. The shape and stacking of the fibres indicate a regular internal secondary shell mosaic pattern made up of alternating rows of smooth, spatulate terminal faces like those in *Spiriferina*. Depositional banding with a periodicity of between 0·15 μm and 0·4 μm was recognized in sectioned fibres of *Retzia* sp. (Pl. 11, fig. 2).

The endopunctate condition of the Retziidina closely resembles that of Recent Terebratulida. In *Homeospira* and *Rhynchospirina* puncta measure about 10 μm in diameter, whereas in *Hustedia* and *Retzia* (Triassic) they measure up to 25 μm. Normally the puncta are unbranched, but with continuing deposition below the crests of ribs, several discrete puncta may gradually encroach upon one another to unite, eventually, as one central canal (Pl. 10, fig. 6). As well as being deflected laterally, secondary layer fibres forming puncta also arch outwards towards the shell exterior. Within the primary layer, the slightly bulbous distal ends of puncta are separated from the shell exterior by a thin canopy of calcite between 2 μm and 4 μm thick (Pl. 11, figs. 3, 4). Although such canopies are grossly recrystallized or broken, it seems reasonable to assume that they were perforated by minute canals such as are found in Recent Terebratulida (Owen and Williams 1969) and *Spiriferina* (MacKinnon 1971a).

(c) Athyrididina

The Athyrididina are divided into two superfamilies, the Athyridacea and Koninckinacea, to include smooth or plicate, short hinged forms with spiralia directed laterally and ventrally respectively. The two superfamilies are easily distinguishable, since Athyridacea are generally biconvex in profile whereas the Koninckinacea include only concavo-convex forms.

(i) *Athyridacea*

The shell structure of early Athyridacea is closely comparable to that of contemporary Atrypacea in that three calcareous shell layers are recognizable. In *Meristella atoka* Girty, from the Haragan Formation at White Mound, Oklahoma, a well-developed primary layer measuring up to 20 μm in thickness can be identified (Pl. 11, fig. 5) and traces of fine transverse banding, which are indicative of periodic deposition, are occasionally preserved. Transverse sections through the shell layers reveal a succession of secondary layer fibres which measure up to 25 μm in width. Judging from the regular stacking of secondary layer fibres which display smoothly curved keels and saddles, it is evident that the internal mosaic comprises alternating rows of terminal faces with arcuate anterior margins. The tertiary layer is exceptionally thick, especially in the pedicle valve (Pl. 11, fig. 6). In sections through the pedicle valve of *Meristina tumida* (Dalman) from the Silurian (Wenlock) of Gotland, tertiary layer crystals stacked normal to the shell surface were found to constitute over 80 per cent of the calcareous shell succession. Traced inwards from the secondary/tertiary layer interface, vertical intercrystalline boundaries are fairly persistent but some appear to die out as a result of amalgamation of adjacent crystals (Pl. 12, fig. 1).

The ventral muscle scars of *Meristella* and *Meristina* are deeply impressed in the postero-median region of the pedicle valve. Transverse sections across the muscle scars reveal that, apart from causing a localized depression on the inner shell surface, the tertiary layer fabric is unaffected. It is evident, however, that shell deposition within muscle scars did not proceed at the same rate as in laterally adjacent areas. The fact that the shell succession is thinner under muscle scars may be attributable to a partial reversal in the secretory behaviour of the outer epithelium from mineral to organic exudation as a means of maintaining adhesion between shell and tissue. In the brachial valve of *Meristella* the dorsal adductor scars are impressed on secondary shell material The myotest fabric produced by the breakdown in secondary shell deposition is very irregular (Pl. 12, fig. 2) and can be traced running posteriorly within the shell succession, and diminishing in extent, towards the umbo.

Many Athyridacea are characterized by the development of a cardinal plate extending across the apical region of the brachial valve. Such a structure, which may be perforated posteriorly, is built up laterally of outer hinge plates and medially of either conjunct inner hinge plates or one single plate. In *Meristella atoka* Girty the cardinal plate is depressed medially and is supported by a median septum which extends forward for half to two-thirds the length of the valve. When sectioned transversely, the structure is Y-shaped, with the base of the letter Y corresponding to the base of the median septum and the crural bases situated at points represented by the other two extremities (Pl. 12, fig. 3). Both the cardinal plate and supporting septum must have grown as one unit in the same way as that described for the *spondylium simplex* of *Skenidioides* by Williams and Rowell (1965 : H114), for the convex faces of secondary layer fibres (keels) are invariably directed away from the median plane of the septum. Growth on the underside of the cardinal plate was continuous with that on the flanks of the median septum and on the upper surface of the cardinal plate which faces toward the pedicle valve. However, as might be expected, part of the shell fabric on the upper side of the cardinal plate, which would be deposited by outer epithelial cells in contact with the dorsal region of the pedicle base, is grossly modified. In a deposit up to 50 μm thick, which coats the upper surface of most of the cardinal plate, the outlines of individual fibres are destroyed and replaced by a highly porous fabric (Pl. 12, fig. 4) which is roughly lineated normal to the shell surface in a manner reminiscent of a primary layer fabric. Apart from the sporadic lineations, it may also be compared with the fabric of the neighbouring dorsal adductor myotest. Presumably the cardinal plate served as the area of attachment for the dorsal ends of the dorsal pedicle adjustor muscles. Indeed, within the brachial valve of *Waltonia inconspicua* (Sowerby), the inner hinge plates unite medially with a septum in a manner identical to that described for *Meristella* ; and on the upper surface of its cardinal plate the secondary mosaic is considerably modified though not as much as in *Meristella*.

In most younger Athyridacea, such as *Athyris* and *Composita*, deposition of a tertiary layer did not occur, and the structure of their primary and secondary layers is unexceptional. The primary layer of *Athyris spiriferoides* (Eaton) from the Upper Hamilton Group (Middle Devonian) of New York measures up to 30 μm in thickness and is composed of vertically stacked crystallites (Pl. 12, fig. 5). It is succeeded by a thick secondary layer composed of orthodoxly stacked fibres with smoothly convex keels and saddles (Pl. 12, fig. 6). Mature fibres measure up to 25 μm in width. The fabric of the primary layer of *Composita ambigua* (Sowerby) from the Calmy Limestone (Lower Carboniferous) of Carluke, Lanarkshire, is the same as that of *Athyris spiriferoides*, and measures up to 20 μm in thickness (Pl. 13, fig. 1). Fibres of the secondary layer are indistinguishable in size and disposition from those of *Athyris*.

Cleiothyridina deroissii (Leveille) from the Blackbyre Limestone (Lower Carboniferous) at Brockley, Lesmahagow, Lanarkshire, excited more interest. It was found to possess a primary layer of up to 25 μm thickness which was succeeded by orthodoxly stacked secondary layer fibres and, like the profiles of secondary layer fibres composing the shells of other Athyridacea, those of *Cleiothyridina* possess smoothly convex keels and saddles (Pl. 13, fig. 2). However, over much of the interior of both valves, secondary layer fibres are succeeded by a thick tertiary layer deposit composed of tall crystals whose basal parts are continuous with the outlines of secondary fibres, as in *Gryphus vitreus* (Born). Of particular interest is the discovery, in sections through the tertiary layer, of a prominent transverse depositional banding which is traceable across adjacent crystal boundaries (Pl. 13, fig. 3). In general the prominence and periodicity of the banding varies greatly. A fairly regular banding with an average periodicity of 900 nm was recognized and taken to reflect diurnal deposition, but even this banding could be subdivided in places into units no more than 200 nm thick.

It is evident from a study of the distribution of the shell layers in *Cleiothyridina* that deposition of all three calcareous shell layers took place simultaneously. However, adjacent parts of the mantle must have been subject to temporary reversals in secretory behaviour, for secondary and tertiary layers interdigitate (Pl. 13, fig. 4), as do primary and secondary layers closer to the contemporaneous valve margins. The fluctuations in primary and secondary shell deposition are more intense than those affecting the tertiary layer and may give rise to a series of frill-like overlapping lamellae which characterize a number of late Palaeozoic Athyridacea. In *Cleiothyridina* the extremities of lamellae are fashioned into long, flat, spinose projections which generally break off when the fossils are extracted from the surrounding rock matrix. Fine spines may also develop upon the frilly edges of overlapping lamellae in *Athyris*.

In certain of the youngest athyridaceans, such as *Diplospirella*, bifurcations of the jugal stem gave rise to a pair of accessory spiral lamellae which grew in such a way as to become intercoiled with the arms of the primary spiralia. Specimens of *Diplospirella wissmani* (Münster) and *Anisactinella quadriplecta* (Münster) from the St Cassian Beds (Triassic) of Northern Italy were examined with a view to determining the skeletal ultrastructure of this stock. In most cases, specimens were small enough for complete valves to be comfortably accommodated on 1·3 cm diameter 'Stereoscan' stubs. In this way, it was possible to view whole shell interiors and thereby interpret the growth of particular areas of interest in relation to the overall fabric.

In sections of *Diplospirella wissmani* (Münster) the primary layer was found to be well preserved (Pl. 13, fig. 5). It is normally about 25 μm thick and exhibits a fine lineation disposed roughly normal to the outer shell surface. In the development of this lineation and its generally porous texture, the primary layer of *Diplospirella* is comparable with that found in living articulates. Transverse growth bands are only sporadically developed. The most striking aspect of the shell structure of *Diplospirella* is the size of secondary layer fibres (Pl. 13, fig. 6; Pl. 14, figs. 1, 2).

Compared with the fibres of *Athyris* or *Composita*, for example, the fibres of *Diplospirella* are exceptionally large and spatulate terminal faces up to 60 μm in width can be discerned even when the valve interiors are viewed under a conventional light microscope. Evidently the outer epithelial cells responsible for secreting the secondary layer of *Diplospirella* were much less mobile than those of most other articulates, for fibres newly proliferated at the valve margins appear to grow radially outwards but those located some distance from the commissure are only slightly reorientated with long axes disposed in such a way as to indicate growth in an anterior direction only. No exceptional twists, spirals or S-shaped convolutions have been observed. The only appreciable modification in the secondary shell mosaic occurs within muscle scars.

Around the anterior margins of scars, the standard secondary shell mosaic breaks down and is replaced posteriorly by a succession of very long exposed trails of fibres bearing no recognizable terminal faces (Pl. 14, fig. 3). Outlines of rather ragged, asymmetrical trails may extend along the scar for more than half its length. This breakdown in the normal process of shell deposition is also recognizable in sections through muscle scars where orthodoxly stacked secondary layer fibres are succeeded inwardly by a succession of fibres with very irregular, though closely interlocking outlines (Pl. 14, fig. 4). In most respects this breakdown in secondary shell deposition within the muscle scars of *Diplospirella* is similar to that which has been observed in young *Notosaria*, except that no arcuate zones of fibres with large terminal faces occur. At the posterior margins of each muscle scar, the long, exposed trails are overlapped by a cluster of very small fibres with terminal faces averaging less than 10 μm in width (Pl. 15, fig. 1). Within a relatively short distance however, the terminal faces of fibres attain dimensions more typical of the secondary layer mosaic pattern which occurs elsewhere on the shell surface. The occurrence of a zone of small fibres around the posterior margins of a muscle scar is important since it provides an indication of the size of outer epithelial cells which must have been located in that part of the shell. Since terminal faces less than 10 μm in width overlap trails which may exceed 60 μm in width, it is evident that a substantial size differential existed between cells located anterior and posterior to the muscle scars. Judging from the way in which the surface level drops around the anterior margins of muscle scars, it would appear that parts of the secondary mosaic which lay in the path of the encroaching muscle base were, to some extent, resorbed. The long exposed trails within muscle scars are interpreted as being remnants of fibres which were involved in resorption when formerly located around the anterior periphery of the scar. Within the muscle scar it is probable that organic membranes completely ensheathed exposed fibre trails, so that the main function of outer epithelial cells underlying muscle bases is likely to have been adhesion and not secretion. Since it is known from a study of living material that the optimum size range for outer epithelial cells underlying muscle bases is substantially less than that outside, it is not surprising to find that the first-formed fibres around the posterior margins of scars are of small dimensions.

The shell structure of *Anisactinella quadriplecta* (Münster) is essentially the same as that recorded for *Diplospirella*. In the only specimen of *Anisactinella* available for study, a thin primary layer consisting of vertically stacked crystals about 8 μm high is preserved (Pl. 15, fig. 2). The secondary layer fibres are large and attain widths of more than 60 μm. Unlike *Diplospirella* the exterior of *Anisactinella* is coarsely plicate, but on the inner shell surface the deposition of secondary layer material within the radially disposed hollows tends to fill out these external irregularities with the formation of a relatively smooth surface.

(ii) *Koninckinacea*

The Koninckinacea as presently constituted comprise six genera of small to medium-sized articulate brachiopods with smooth concavo-convex shells which enclose a double pair of ventrally directed spires. Despite the distinctive external shell morphology and an unusual brachidium, the superfamily has received little attention since the end of the nineteenth century. With the exception of *Cadomella*, the genera are perhaps best known as representatives of the Triassic St Cassian fauna of the Italian Dolomites so extensively collected and figured by Bittner (1890 : 304–309). It was not until Cowen and Rudwick (1966 : 403–406) discovered a spiral brachidium in *Cadomella davidsoni* (Eudes-Deslongchamps) that this Lower Jurassic genus was recognized as a member of the Koninckinacea.

In the *Treatise* (1965 : H666) Boucot *et al.* assign the Koninckinacea and Athyridacea to the suborder Athyrididina and the spiriferide affinities of the koninckinaceans were not questioned until Cowen and Rudwick proposed a rearrangement of this existing classification, based on general shell morphology, with the transference of the superfamily, amended to include *Cadomella*, from the Spiriferida to the Strophomenida. However, the strongly concavo-convex shell profile and the morphology of the apical region, though reminiscent of many Strophomenida, are not diagnostic features. In addition, the statement made by Cowen and Rudwick (1966 : 404) that the pedicle foramina of *Koninckella liassina* Bouchard, *K. triassina* Bittner and *Amphiclina suessi* Laube 'are definitely supra-apical' is not supported by recent observations on *K. triassina* Bittner, *Amphiclina amoena* Bittner, *Cadomella davidsoni* (Eudes-Deslongchamps) and *C. moorei* (Davidson) made by Brunton and MacKinnon (1972 : 410). As will be shown presently, the nature of the calcareous shell succession in Koninckinacea is comparable with that of a number of Spiriferida, but quite unlike that of any Chonetidina (Williams 1968a : 46) ; therefore, in the absence of any morphological detail, macroscopic or microscopic, that would serve to establish strophomenide identity, there now appears to be no valid reason for removing the Koninckinacea from the Spiriferida.

This account of the shell ultrastructure of the Koninckinacea is based on an examination of specimens belonging to three genera : *Koninckina leonhardi* (Wissman) and *Amphiclina amoena* Bittner from the St Cassian Beds (Triassic) of Northern Italy, and *Cadomella davidsoni* (Eudes-Deslongchamps) and *C. moorei* (Davidson) from Liassic clays near Caen, France.

The primary layer of *Koninckina* is about 10 to 12 μm thick. In transverse section it is usually discernible as a series of closely packed crystallites between 0·5 μm and 2·0 μm in width which are stacked normal to the isotopic boundary between the primary and secondary shell layers (Pl. 15, fig. 3). On the outer shell surface, faint concentric growth lines cut across a fine radial lineation (Pl. 15, fig. 4) which appears at higher magnifications to be a series of narrow troughs and ridges. The ridges are comparable in width and stacking to that of the crystallites observed in thin section, and because of their consistency and regular spacing are considered to be an original feature of the outer shell surface. Presumably the inner bounding membrane of the periostracum, which must have provided an outer organic cover to both valves, was moulded by crystal growth into a series of radial grooves and fine ridges corresponding in negative to the undulations on the shell surface. Possibly organic strands or membranes extended through the primary layer by way of the spaces between crystallites to join up with the organic components of the secondary shell layer. Apart from being slightly thicker, the primary layer of *Amphiclina* is little different from that of *Koninckina*.

Williams (1968a : 34) noted that the secondary layer of *Koninckina* is composed of fibres which grow to an unusually large size in comparison with the secondary layer fibres of most other articulates. On the internal surfaces of both valves the terminal faces of secondary layer fibres are rhomb-shaped (Pl. 15, fig. 5) and not spatulate as is common in Recent Terebratulida, Rhynchonellida and some Spiriferida. This distinctive secondary shell mosaic pattern has the general appearance of diagonally intersecting rows of rhomb-shaped faces but such rows are not perfectly

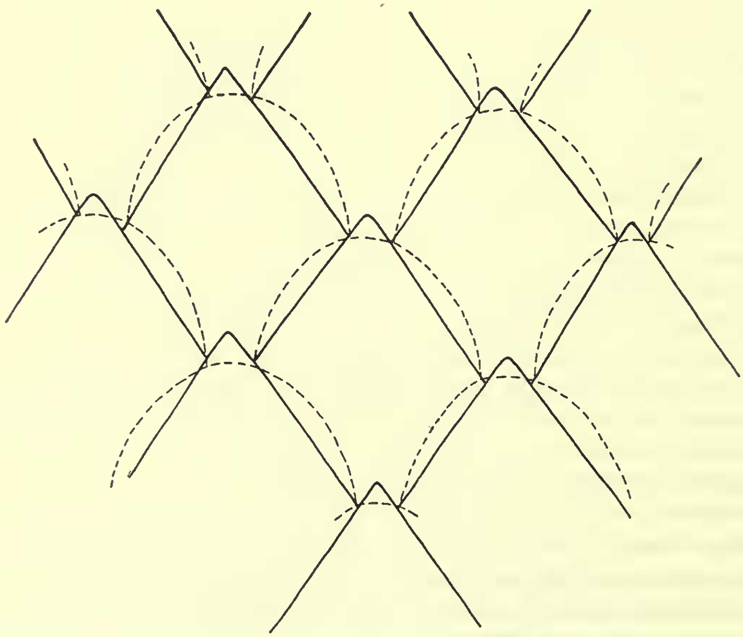

FIG. 13. Plan of the secondary shell mosaic on the internal surface of a valve of *Koninckina*, showing the diamond-shaped outlines of terminal faces. The more normal, smoothly curved mosaic, such as is found in Recent Rhynchonellida and Terebratulida, is shown by broken lines for comparison.

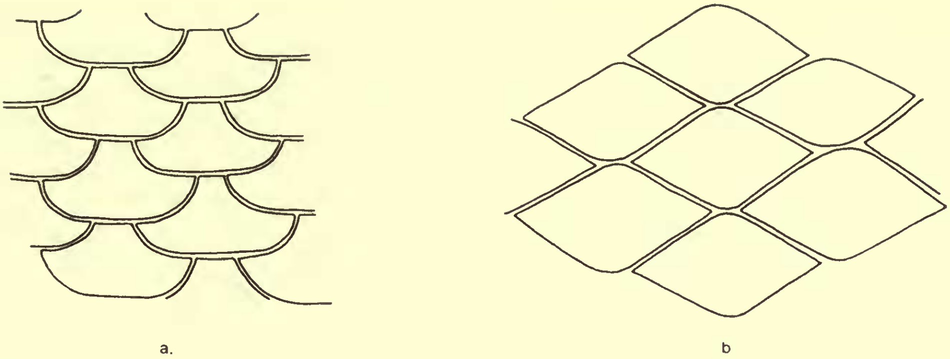

FIG. 14. a. Stylized transverse section of the secondary shell of a Recent rhynchonellide or terebratulide showing the characteristic shape and stacking of fibres. b. Stylized transverse section of the secondary shell of *Koninckina* showing the characteristic diamond-shaped outlines of fibres.

linear, as the outline of each terminal face is displaced fractionally from its neighbours. To derive this internal surface pattern from the more typical spatulate mosaic requires only a sharpening of the arcuate junction between the calcite and protein secretory zones in the overlying outer epithelium (Text-fig. 13). Diamond-shaped terminal faces with diagonal lengths and widths measuring up to 45 μm and 30 μm respectively have been observed in both *Koninckina* and *Amphiclina* (Pl. 15, fig. 6).

The shape and stacking of secondary layer fibres in transverse section are dependent initially on the slope and spatial relationships of the corresponding outer epithelial cells on the inner shell surface. For example, in a Recent rhynchonellide or terebratulide, cross sections of a typical fibre show that it is bounded by an inwardly curved surface (the keel) which is truncated by an outer one made up of two curved lateral areas and one median depression (the saddle) (Text-fig. 14a). The profile of the inner and outer surfaces of a fibre correspond to the foreshortened outlines of the anterior and posterior boundaries of the terminal face. Since both the anterior as well as the posterior boundaries on the terminal face of the koninckinacean secondary layer fibre are angular, the cross-sectional outline of the fibre is correspondingly modified. Transverse sections of *Koninckina* and *Amphiclina* reveal that the fibres are roughly diamond-shaped with inner and outer surfaces variably truncated (Text-fig. 14b).

In some, if not all, specimens of *Koninckina* recovered from the St Cassian beds, the secondary shell fabric is almost certainly original because fibres in longitudinal and transverse sections exhibit a fine depositional banding (Pl. 16, figs. 1, 2) of variable periodicity, which probably represents slight fluctuations in the physiological behaviour of the corresponding outer epithelial cells. The mean periodicity of 37 bands measured from cross-sections of six adjacent fibres was 0·89 μm (range 0·58 μm to 1·54 μm). However, until more is known of the factors controlling mineral secretion in living brachiopods, such as the effects of temperature, light and salinity of the local environment, feeding habits, availability of food, tidal conditions, etc., the precise significance of such depositional features must remain in some doubt.

Some distance in from the shell edge of *Koninckina* and *Amphiclina*, the secondary layer fibres are succeeded by a tertiary layer deposit which thickens towards the centre of both valves. The change-over from secondary to tertiary deposition corresponds with the anterior extremities of the primary lamellae which comprise the first and broadest convolution of the spiral brachidium. Posterior to this line, the narrow shell cavity is moulded to the shape of the two shallow, ventrally directed coils, thus producing a dome-shaped swelling (Pl. 16, fig. 3) on either side of the brachial valve mid-line and a pair of depressions in the pedicle valve. Superimposed on each outgrowth (or depression) is a spiral groove along which are channelled the arms of the spiralia. In addition, the shell surface is pock-marked by a number of shallow pits which appear in some parts to be distributed along the spiral grooves. However, it seems unlikely that the pits are related to any part of the brachial structure, and an interpretation favouring some form of gonadal markings (such as are commonly found in *Atrypa*) seems more plausible. Impressions related to brachidia (and gonads) have been observed in both *Koninckina* and *Amphiclina*.

An examination of the tertiary layer in *Koninckina*, in plan as well as in section, reveals a shell fabric closely comparable with that observed in living *Gryphus*. The secondary shell mosaic, with its distinctive diamond-shaped terminal faces, breaks down into a grossly modified surface pattern which appears as an irregularly anastomosing network of intercrystalline boundaries (Pl. 16, fig. 4). The rough undulating topography of each growing face contrasts with the smoothness of the secondary layer terminal faces. Dimensions of faces are difficult to measure, because of their irregularity in outline, and a better estimate of their dimensions can be made from sections cut at right angles to the plane of growth. Seen in depth, the tertiary layer is composed of vertically stacked and tightly interlocking columns of calcite, separated from one another by clear-cut boundaries (Pl. 16, fig. 5). Although the isotopic boundary between the secondary and tertiary layers is well defined, it is evident that the vertically stacked columns grew in continuity with the underlying secondary fibres. There is a one-to-one correspondence between tertiary layer columns and secondary layer fibres for, in longitudinal sections showing the secondary/tertiary layer junction, each rod-like fibre of the secondary layer gives rise to a single vertical column (Pl. 16, fig. 6).

The mode of formation of the tertiary layer in *Koninckina* must have been very similar to that occurring in living *Gryphus*. At a certain distance from the shell edge, the outer epithelial cells ceased to migrate in the horizontal plane but continued to secrete calcite, so that a thick deposit was laid down normal to the shell surface. Over certain parts of the inner shell surface of *Koninckina*, notably the posteromedian region behind muscle scars, there is a regrowth of the secondary layer fibres on top of the tertiary layer. Generally one tertiary layer column will be succeeded by one fibre but sometimes two or rarely three branches emerge at this inner isotopic boundary.

(d) Spiriferidina

The Spiriferidina constitute the largest and most diverse suborder of all spire-bearing brachiopods. In general the spiriferidine shell is broadly strophic and possesses a well-developed ventral interarea. The spiralia are directed laterally or postero-laterally.

The problems of spiriferid classification are well summed up by George (1933 : 423–456) who recognized the lack of reliable morphological criteria on which a workable and satisfactory scheme could be founded. In the *Treatise* classification, Pitrat (1965 : H667) considered the existence of longitudinal striations on the cardinal process to be a feature of critical importance. Using this fact as his main basis for suprageneric classification, he separated the 'non-striate' Cyrtiacea (impunctate) and Suessiacea (punctate) from the 'striate' Spiriferacea (generally impunctate, plicate), Reticularacea (impunctate, smooth) and Spiriferinacea (punctate).

(i) *Cyrtiacea*

The Cyrtiacea as defined in the *Treatise* (1965 : H667) include the Eospiriferinae and their impunctate derivatives, the Cyrtiinae and the Ambocoeliidae. Specimens of *Eospirifer*, the earliest cyrtiacean, were unavailable for study but sections of the related genus *Cyrtia exporrecta* (Wahlenberg) from the Silurian of Coalbrookdale, Shropshire, reveal a thin, recrystallized primary layer measuring up to 10 μm in thickness. Fibres of the secondary layer are unlike those of contemporary Atrypidina in that they exhibit symmetrical profiles with rounded keels and saddles instead of being diamond-shaped (Pl. 17, fig. 1). From the regular stacking of fibres and their smooth outlines, it can be deduced that the internal mosaic consists of alternating rows of broadly spatulate terminal faces. On average, fibres measure about 12 μm in width.

The Eospiriferinae and the Cyrtiinae are thought to be very closely related, since the two groups are substantially the same except for overall shell shape and modifications of the delthyrium (Pitrat 1965 : H667). The smooth-shelled, generally planoconvex Ambocoeliidae are less emphatically related to the other two subfamilies, but are grouped with them mainly on account of their possession of a non-striate cardinal process.

Ambocoelia umbonata (Conrad) from the Hamilton Group (Middle Devonian) of New York possesses a well-developed primary layer up to 40 μm thick which is best preserved around the commissures of mature specimens. In this area, primary and secondary shell layers interdigitate as the two major components of overlapping growth lamellae (Pl. 17, fig. 2). The curved outlines of secondary layer fibres in section indicate an orthodox secondary shell mosaic pattern with terminal faces about 20 μm wide (Pl. 17, fig. 3). In the vicinity of muscle scars the regular stacking of fibres breaks down and outlines of adjacent fibres become ragged and impersistently welded together. The interior of a brachial valve of the related genus, *Crurithyris* sp. from the Finis Shale (Pennsylvanian) of Texas, was sufficiently free from enclosing rock matrix to allow examination of the surface mosaic. As might be expected, the surface was badly etched and pitted but the outlines of individual secondary layer terminal faces, on average 20 μm wide, were still recognizable (Pl. 17, fig. 4). In the umbonal region of the brachial valve a narrow cardinal process lies between two prominent, inwardly convex inner socket ridges (Pl. 17, fig. 5). The base of the cardinal process is cylindroid and rises posteriorly to become densely tuberculate (Pl. 17, fig. 6), but no longitudinal striation, such as was found in *Spiriferina*, could be detected.

(ii) *Suessiacea*

Apart from the monotypic genus *Suessia* which constitutes the family Suessidae, the Suessiacea includes representatives of the family Cyrtinidae. Most genera are punctate and characterized by a weakly convex brachial valve and hemipyramidal pedicle valve. Although resembling most Cyrtiacea in the possession of a nonstriate cardinal process as well as in external morphology they differ mainly in the development of a ventral median septum and dental plates which may merge to form a spondylium-like structure.

Two species of *Cyrtina* were examined in order to help determine the skeletal fabric of the superfamily. Specimens of *Cyrtina alpenensis* Hall and Clarke, from the Middle Devonian of Rockport, Alpena County, Michigan, possess well-developed primary and secondary shell layers. The primary layer, on average about 20 μm thick, has a spongy appearance and is traversed by a faint lineation disposed normal to the shell exterior (Pl. 18, fig. 1). Fibres of the secondary layer are small, presenting a mean width of 10 μm. In both valves the secondary layer fibres are outwardly deflected around puncta which may measure up to 25 μm in diameter. The puncta appear to penetrate the primary layer, but due to the homogeneity of the sedimentary infilling of puncta with the fabric of the primary layer, it was impossible to distinguish any distal coverings. Branching puncta may occur sporadically in both valves.

On the interior of the pedicle valve, the dental plates are strongly developed and converge rapidly to unite with a high, blade-like median septum. The septum of *Cyrtina* is unusual in that it supports a narrow medially partitioned chamber along its posterior facing edge. This chamber, the tichorhinum, extends from the umbo to the dorsal edge of the median septum and is subtended laterally by the inner surface of the dental plates. In some species of *Cyrtina* the tichorhinum is reported to be incompletely partitioned (Amsden 1958 : 135). In transverse sections of *Cyrtina* sp. from the Upper Devonian of Rockford, Iowa, the tichorhinum is seen to originate as a bulbous triple-branched extension of the median septum comprising one median partition and two lateral, curved walls (Pl. 18, fig. 2). Judging from the disposition of secondary layer fibres which tend to run parallel to the long axis of the tube, it is evident that the tichorhinum was fashioned as a result of the localized evagination of outer epithelium situated on both sides of the postero-dorsal edge of the median septum. The reasons for evagination having occurred in the first place are not clear, but it is evident that the greater part of the median septum served as a muscle attachment area. Two discrete myotest shell fabrics are recognizable in transverse sections through the median septum (Text-fig. 15). The first is situated close to the median plane of the septum and is overlapped by a subsequent deposit of

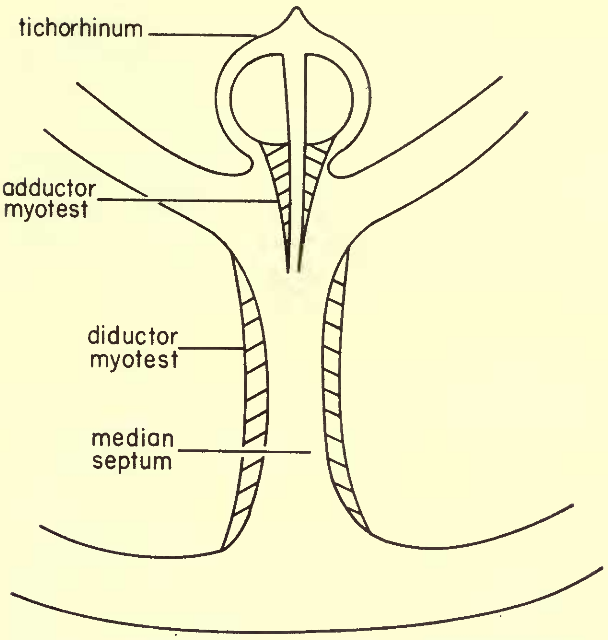

FIG. 15. Stylized transverse section through the ventral median septum and tichorhinum of *Cyrtina*, showing the distribution of myotest.

secondary shell material. Above the level of the fused dental plates this myotest can be traced running into the tichorhinum. The second myotest is situated on either side of the septum below its junction with the dental plates and extends as far as the floor of the valve (Pl. 18, fig. 3). Since the first myotest is unaffected by the union of the dental plates, it is evident that its former position of growth was located forwards (and dorsal) of the point where the dental plates join with the septum. This would correspond to a position on the septum which is situated at its postero-dorsal extremity close to the hinge line. Since the second myotest is located on the flanks of the septum below the dental plates, it must comprise part of a muscle scar which is impressed further back on the septum at a lower level within the hemi-pyramidal pedicle valve.

Despite its unusual pedicle valve morphology, the musculature of *Cyrtina* was probably no different from that of other articulate brachiopods. Certainly the emplacement of muscles in the brachial valve was quite orthodox. On the floor of the brachial valve are two pairs of adductor scars with a bilobed cardinal process situated in the umbonal region (Hall and Clarke, 1894 : 763). The muscle scar layout in the pedicle valve of *Cyrtina* can best be understood by making direct comparison with the pedicle valve musculature in Recent genera (Text-fig. 16a, b). In *Notosaria*, for example, two small adductor scars are bordered antero-laterally by the ventral diductor and adjustor scars. Extending this arrangement to *Cyrtina*, it seems most likely that the ventral ends of the adductors were inserted within the tichorhinum as well as being attached to the postero-dorsal part of the septum, and that the diductors ran obliquely forward from the cardinal process to attach to the antero-lateral parts of the median septum (Text-fig. 16c). The ventral adjustor muscles were probably attached to the antero-lateral surface of the dental plates.

The transference of the areas of ventral muscle attachment to a median septum was accompanied by an adjustment in the structure of the spiral brachidium. The innermost coils of both calcareous spires of *Cyrtina* are situated very close to one another and joined by a sharply pointed, anteriorly directed jugum (Text-fig. 17a, b). The apices of the spiralia are directed obliquely posterior and extend well within the lateral cavities of the hemipyramidal pedicle valve.

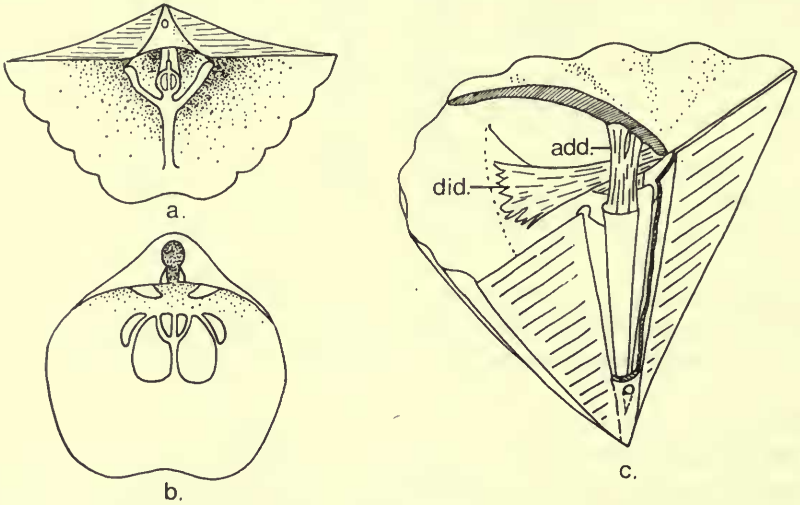

FIG. 16. a, b. Views of the interiors of the pedicle valves of *Cyrtina* (a) and a more conventional articulate such as *Notosaria* (b), showing the relative location of muscle attachment areas. c. Cut-away diagram of *Cyrtina* showing the inferred restoration of the adductor and diductor muscle systems.

(iii) *Spiriferacea*

The Spiriferacea is by far the largest of the five superfamilies comprising the Spiriferidina. Their shell form is variable but in general it tends to be rather transverse with either angular or slightly rounded cardinal extremities. In most cases maximum width is attained across the hinge line, but in some forms, such as the Brachythyrididae, the hinge line is substantially short of maximum width. The earliest Spiriferacea such as *Delthyris* and *Howellella* appeared at much the same time (Lower Silurian) as the first cyrtiaceans *Cyrtia* and *Eospirifer*. In such early genera, lateral plications are few and the fold and sulcus are generally smooth; however, in later Spiriferacea costation became more intense and varied as did the nature of concentric growth lamellae. In addition, there was considerable variation in the development of the finer elements of the surface ornament, such as spines, granules and capillae.

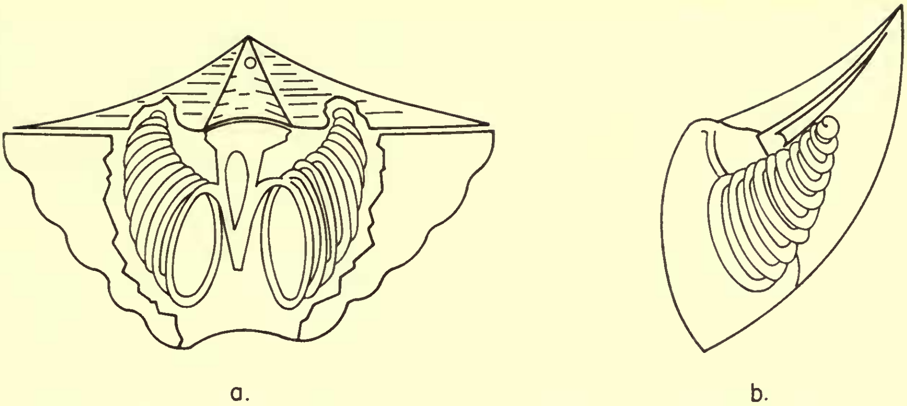

FIG. 17. Dorsal (a) and lateral (b) views of *Cyrtina* showing the disposition of the spiral brachidium.

The shell structures of two genera assigned to the Delthyridae were investigated. These were *Delthyris saffordi* (Hall) from the Brownsport Formation (Upper Silurian) of Western Tennessee and *Kozlowskiellina velata* (Amsden) from the Haragan Formation (Lower Devonian) at White Mound, Murray County, Oklahoma. No recognizable primary layer was preserved in *Delthyris*, but the fibres of the secondary layer, measuring up to 25 μm in width, displayed smoothly curved outlines of keels and saddles (Pl. 18, fig. 4). The regular stacking of fibres as seen in transverse section indicates the development of an internal surface mosaic comparable with that observed in *Spiriferina*. Some sections through fibres reveal traces of a transverse banding with an average periodicity of about 0·4 μm, which is considered to be depositional. In *Kozlowskiellina* a primary layer measuring up to 10 μm in thickness is preserved (Pl. 18, fig. 5). The shape and stacking of transversely sectioned secondary layer fibres, which measure on average 20 μm in width, point to an internal secondary shell mosaic pattern consisting of alternating rows of terminal faces with smooth spatulate outlines (Pl. 18, fig. 6). In the posterior parts of both valves, in particular the pedicle valve, the secondary layer attains considerable thickness. In some instances earlier-formed parts of exoskeletal outgrowths such as the crura and ventral median septum may be identified by the distinctive stacking of their fibres. Transverse sections through a crus of *Kozlowskiellina* reveal that it grew in much the same way as that described for the same structure in Recent Terebratulida and Rhynchonellida, with the growth of fibres along its length (Pl. 19, figs. 1, 2, 3). The fibres are so arranged as to indicate deposition on the ventro-lateral side of the crus only, with the dorso-median facing side exposing long trails without terminal faces (cf. Williams 1968a : text-fig. 12, p. 17). In both the brachial and pedicle valves of *Kozlowskiellina* a myotest shell fabric could be recognized. For example, within the ventral diductor myotest there is a sudden breakdown in normal secondary shell deposition with the replacement of orthodoxly stacked fibres by an irregular, semi-granular accretion of calcite forming a layer about 50 μm thick (Pl. 19, fig. 4). The first few rows of secondary layer fibres which succeed the myotest deposit are noticeably small, being less than 10 μm in width. In this respect they are comparable with the narrow zone of small fibres which overlap the posterior margins of muscle scars in *Notosaria.* Normal secondary shell growth does not become fully re-established behind the ventral diductor myotest, for transverse sections reveal the subsequent deposition of a semiprismatic layer of considerable thickness. This deposit resembles, in places, the 'jigsaw-puzzle' type of shell fabric that characterizes the tertiary layer of *Dayia navicula* (Sowerby).

While not showing the widespread development or regularity of the tertiary layer of living *Gryphus,* this localized deposit in *Kozlowskiellina* is quite distinct from the secondary layer which incorporates all exoskeletal outgrowths as well as adjacent parts of the valve floor. The location of the deposit may provide some clue as to its origin. Outer epithelial cells which secrete secondary layer fibres are known to migrate laterally across the floors of valves leaving trails of calcite marking the routes along which they proceed. It is possible that those outer epithelial cells situated behind the ventral muscle bases of *Kozlowskiellina* were unable to migrate forwards or laterally fast enough and thus contributed to the build-up of shell material which was deposited in a plane roughly normal to the inner shell surface. This hypothesis, however, can only be used in an attempt to explain the development of a tertiary shell fabric behind muscle scars in forms such as *Kozlowskiellina,* and not the widespread tertiary layer deposit as is found in other Spiriferida like *Cleiothyridina.*

The discovery of this incipient tertiary layer in *Kozlowskiellina* poses the question as to whether such a deposit is characteristic of other related genera. Unfortunately no other specimens were available for comparison under the scanning electron microscope, although Krans (1965) has examined the shell structure of a number of Delthyridae by means of cellulose acetate peels. In a study which included Devonian species of *Howellella, Howittia, Hysterolites, Spinella, Paraspirifer, Brachyspirifer* and *Euryspirifer,* Krans reports the growth and development of only two calcareous shell layers, the primary and secondary layers. From the primitive delthyrid stock are descended a large number of Spiriferacea which are subdivided, on the basis of differences on external and internal morphology, into eight other families.

The shell exterior of *Mucrospirifer* sp. from the Middle Devonian of Michigan is covered by a primary layer about 12 μm thick which is lineated normal to the isotopic boundary between the primary and secondary layers (Pl. 20, fig. 1). The first few rows of secondary layer fibres are small, measuring less than 8 μm in width, but when traced further inwards they show an increase in size to a maximum of 15 μm width. All fibres are orthodoxly stacked and display evenly curved keels and saddles (Pl. 20, fig. 2).

No specimens of *Fimbrispirifer* were available for study, but Krans (1965, pl. 9, figs. 3, 6) figures sections of two species from the Devonian of Spain which appear to possess a standard primary and secondary shell succession.

The shell structure of *Spinocyrtia* sp. from the Middle Devonian of Michigan is unexceptional. It possesses a recrystallized primary layer which measures about 12 μm in thickness (Pl. 20, fig. 3). Fibres of the secondary layer, although comparable in shape and stacking with those of *Mucrospirifer,* are generally smaller.

Young fibres which succeed the narrow zone of primary shell deposition located around the shell edge are generally about 4 μm wide, but mature fibres which are laid down well within the shell interior attain, on average, a width of 10 μm (Pl. 20, fig. 4).

Only fragments of a pedicle valve of *Syringothyris cuspidata* (Martin) from the Lower Carboniferous of Staffordshire were obtainable for the purpose of sectioning. Parts of fibrous secondary layer were recognizable (Pl. 20, fig. 5) but no primary layer was present. *Syringothyris* differs from all other Spiriferacea in being penetrated by puncta measuring up to 20 μm in diameter around which the secondary layer fibres are outwardly deflected (Pl. 20, fig. 6). Sass (1967 : 1244) has investigated the shell structure of six species of *Syringothyris* and found all of them to be punctate. In addition, he reports that the shell of *Syringothyris* comprises three calcareous layers, namely the primary, secondary and prismatic (tertiary) layers. Within the tertiary layer the puncta are traceable as irregular passageways which run along the boundaries of adjacent crystal faces (Sass 1967 : 1244). Certain generally impunctate spire-bearing brachiopods (Licharewiinae), which are found in beds of Upper Carboniferous and Permian age, are also assigned to the family Syringothyridae by Pitrat (1965 : H692). In most cases they appear to be morphologically indistinguishable from the Spinocyrtiidae but as the last surviving representatives of this family are considered to have become extinct during the late Devonian, direct descent of the Licharewiinae from such a stock is considered unlikely. Armstrong (1968a : 183) found only two calcareous shell layers in the punctate genus *Subansiria* from the Permian of Australia.

Investigations of the shell structure of the Devonian Costispiriferidae were confined to the finely ribbed form, *Theodossia hungerfordi* (Hall) from the Hackberry Stage (Upper Devonian) of Iowa. The primary layer, which may be up to 25 μm thick, is succeeded by regularly stacked secondary layer fibres which attain a width of about 10 μm. Exoskeletal outgrowths such as teeth and spiralia (Pl. 21, fig. 1) are built up from secondary layer fibres. In the postero-median parts of the shell a tertiary layer is developed. This thick inner layer consists of well-defined narrow crystals on average about 10 μm in width which are stacked normal to the inner shell surface (Pl. 21, fig. 2).

The shell structure of two representatives of the Costispiriferidae were investigated. These were *Tenticospirifer cyrtiniformis* (Hall and Whitfield) from the Hackberry Stage (Upper Devonian) of Iowa, and *Syringospira prima* Kindle from the Percha Formation (Upper Devonian) of New Mexico. In both valves of *Tenticospirifer* the calcareous shell succession was found to be in a particularly good state of preservation. The primary layer which may measure up to 45 μm in thickness has a porous texture and bears traces of a faint lineation disposed normal to the shell exterior (Pl. 21, fig. 3). Fibres of the secondary layer measure, on average, 10 μm in width but although outlines of fibres appear in transverse section to be flattened in the style of *Hemithiris* (Williams 1971b : pl. 1, fig. 3b), they are nonetheless orthodoxly stacked (Pl. 21, fig. 4). This levelling out of keels and saddles is considered to reflect a slight change in the profiles of terminal faces from spatulate to sub-rectangular in outline. Within the vicinity of muscle scars, the standard secondary layer fabric

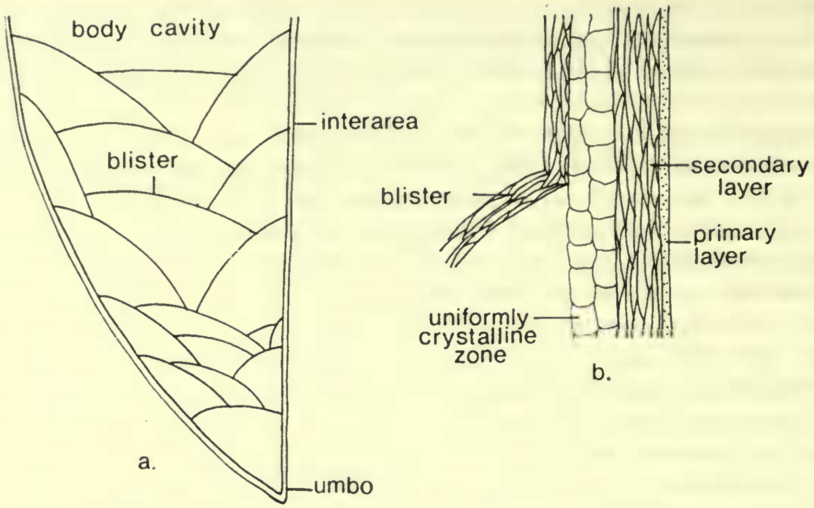

FIG. 18. a. Longitudinal section through a pedicle valve of *Syringospira* showing the development of a series of overlapping partitions. b. Stylized section through a partition and shell wall of *Syringospira* showing the intervening uniformly crystalline zone.

is grossly affected and the boundaries between myotest and earlier-formed parts of the shell succession are abrupt. The ultrastructure of the myotest is difficult to decipher but judging from its semigranular appearance in transverse section (Pl. 21, fig. 5) it is probably composed of small irregular fibres which are impersistently welded together in a manner reminiscent of the ventral myotest of *Notosaria*. *Syringospira*, like *Tenticospirifer*, possesses a well-developed primary layer which may measure up to 40 μm in thickness. Sections through the primary layer reveal a dense vertical striation on which there is superimposed a spongy fabric (Pl. 21, fig. 6). Secondary layer fibres are narrow and seldom exceed 10 μm in width. Shell growth in *Syringospira* was accompanied by the development of a succession of overlapping partitions (Text-fig. 18a) within the umbonal cavities of both valves (Cooper 1954 : 328). The ultrastructure and mode of formation of these blister-like plates have already been described by Williams (1971a : 66). Each blister is composed of conventional secondary layer fibres. Williams' view that secretion of an organic seeding shell preceded the deposition of fibres away from the valve floor is supported by the discovery of a uniformly crystallized zone, up to 35 μm wide, which lies sandwiched between the junction of two adjacent partitions (Pl. 22, fig. 1 ; Text-fig. 18b).

A temporary reversion to wholly organic exudation is by no means unlikely for similar changes in secretory behaviour are known to occur periodically in living Rhynchonellida and Terebratulida. Organic layers, believed to be composed of protein, have been found within the calcareous shell succession of *Hemithiris psittacea* (Gmelin). As such deposits tend to be exuded over the entire shell surface the optical properties of the total shell fabric become affected. Valves of *Hemithiris* which possess organic interlayers are invariably black in colour. In the terebratulide *Magasella sanguinea* (Leach) exudation of a thin organic layer facilitated the backward slide of the mantle edge during its periodic retractions (Williams 1971a : 64). A temporary reversal to organic deposition may have served much the same function in *Syringospira* as it does, at present, in *Magasella*. Just as the terebratulide mantle becomes detached from the adjacent shell surface (caeca included) so also is it likely that the mantle of *Syringospira* detached itself in part from the remainder of the valve floor. The space created by this movement may have become temporarily filled with fluid but in any case it is likely that exudation of a temporary organic covering followed in order to seal off the space and provide a convenient seeding sheet for the secretion of a more rigid partition composed of secondary layer fibres and their organic sheaths.

The shell structure of the family Spiriferidae, as represented by *Spirifer trigonalis* Martin from the Lower Carboniferous of Lanarkshire and *Neospirifer cameratus* (Morton) from the La Salle Limestone (Pennsylvanian) of Ohio, is variable. In *Neospirifer*, primary and secondary shell layers are clearly recognizable (Pl. 22, fig. 2). The primary layer which measures up to 40 μm in thickness is similar in texture to the primary layer of *Tenticospirifer*. It is rather porous and lineated normal to the outer shell surface. Fibres comprising the secondary layer are orthodoxly stacked and measure up to 15 μm in width. The calcareous shell succession of *S. trigonalis* differs from that of most other Spiriferacea in that it incorporates a well-developed tertiary layer. Three shell layers were first recognized in *S. trigonalis* by Dunlop (1962 : 483) who named them the lamellar (primary) layer, fibrous (secondary) layer and columnar (tertiary) layer. A 'Stereoscan' examination of both valves of *S. trigonalis* confirms most of Dunlop's findings. A primary layer about 15 μm thick is succeeded by a secondary layer of fibres, on average 20 μm wide, which are roughly diamond-shaped in profile (Pl. 22, fig. 3). Vertically stacked crystals comprising the tertiary layer of *S. trigonalis* occupy the greater part of the interior of both valves (Pl. 22, fig. 4). Towards the periphery of both valves secondary and tertiary layers may interdigitate (Pl. 22, fig. 5). Dunlop's view (1962 : 488) that the interlayering is due to fluctuations in the rate of shell growth is supported by my own observations. However, there are no sharp depositional breaks at any junction between secondary and tertiary layers, as Dunlop supposes, but occasionally slight variations in chemical composition of parts of the tertiary layer may produce, on etching, prominent growth lines which might be interpreted as such at lower magnifications. The tertiary layer fabric is grossly affected in the vicinity of muscle scars. Sections through a ventral muscle scar of one specimen of *S. trigonalis* reveal a myotest comprising narrow, irregular fibrous outlines, which in places almost tends to become finely granular (Pl. 22, fig. 6).

Representatives of the family Brachythyrididae differ from those of the family Spiriferidae mainly in being less transverse, with the width of the hinge line generally falling well short of maximum width. A well-preserved specimen of *Choristites mosquensis* Buckman from the Upper Carboniferous of the Moscow region, U.S.S.R., was used to determine the skeletal fabric of the family. The shell structure of *Choristites* is similar to that of *Spirifer trigonalis* in that three calcareous shell layers are present. The primary layer, measuring up to 25 μm thick, is normally recrystallized but it can still be recognized in sections as a uniform band of narrow, vertically stacked crystals which blanket the outer surface of both valves (Pl. 23, fig. 1). The secondary and tertiary layers, by contrast, are well preserved. In transverse sections, the secondary layer is seen to be built up of orthodoxly stacked fibres, averaging 10 μm in width, which display smoothly curved keels and saddles (Pl. 23, fig. 2). In both pedicle and brachial valves, the secondary layer is succeeded by a well-developed tertiary layer deposit (Pl. 23, fig. 3). The vertically stacked crystals of the tertiary layer may vary from 10 μm to more than 20 μm in width, due presumably to occasional localized breakdowns in the deposition of bounding organic membranes which may allow two or three adjacent crystals to merge as one. Nevertheless, the boundaries between crystals are normally upright, so it can be assumed that, during deposition of the tertiary layer, little or no lateral migration of outer epithelial cells took place. The tertiary layer of *Choristites* is characterized by a prominent transverse depositional banding with an average periodicity of 2 μm. Within each 2 μm-deep band, several more indistinct transverse bands may occur (Pl. 23, fig. 4). Approximately five minor bands may fit within one 2 μm band, giving an average periodicity for the minor banding of 0·4 μm. The latter value is consistent with measurements of fine depositional bandings recorded within the tertiary layers of other Spiriferida (and also *Gryphus*) and is thus considered to be diurnal. It is tempting, therefore, to rationalize the more prominent 2 μm bands in *Choristites* in terms of some other less frequent, yet still regular influence, such as fluctuating tidal behaviour. The secondary and tertiary layers of *Choristites* are seen to interdigitate frequently, as in *S. trigonalis* (Pl. 23, fig. 5). Muscle emplacement also gave rise to modifications in skeletal fabric similar to those observed in *S. trigonalis*. In the vicinity of muscle scars, the standard secondary or tertiary layers are disrupted and replaced by a deposit about 30 μm thick consisting of small, irregularly stacked fibres which may, in places, become more massive due to the welding together of adjacent margins (Pl. 23, fig. 6).

For comparison with *Choristites*, a specimen of *Brachythyris* sp. from the Lower Carboniferous of Kildare, Ireland, was sectioned. Although both valves proved to be badly altered, localized patches of secondary and tertiary layer deposits were positively recognized and allowed the calcareous shell succession for that genus to be established (Pl. 24, figs. 1, 2). In most respects, the calcareous shell succession of *Brachythyris* appears to be the same as that described for *Choristites*.

(iv) *Spiriferinacea*

The shell structures of three Carboniferous representatives of the Spiriferinacea were investigated with a view to making a general comparison with the standard shell succession of *Spiriferina walcotti*. These were *Crenispirifer* sp. from the La Salle Limestone (Pennsylvanian) of Ohio, and *Punctospirifer scabricosta* North and a specimen labelled as '*Spiriferina cristata* var. *octoplicata*' (tentatively referred to *Spiriferellina cristata* (Schlotheim)), both from Ashfell, Westmorland. Of these three, '*S. crista* var. *octoplicata*' was the least well preserved. A section through the pedicle valve of this specimen exposed a secondary layer built up of irregular fibres which measure, on average, 12 μm in width. The fibres are outwardly deflected to form cylindroid canals (puncta) which have a mean diameter of 20 μm (Pl. 24, fig. 3). No primary layer was preserved.

The shell of *Punctospirifer scabricosta* North was somewhat better preserved than that of the *S. cristata*, and a primary layer measuring 25 μm in thickness was clearly recognizable (Pl. 24, fig. 4). Fibres of the secondary layer are orthodoxly stacked and exhibit smoothly rounded keels and saddles like *S. walcotti* (Pl. 24, fig. 5). The puncta measure up to 30 μm diameter (Pl. 24, fig. 6).

The *Crenispirifer* sp. proved to be the most useful specimen for comparison with *S. walcotti*. Both primary and secondary shell layers are well preserved. The primary layer, which has a spongy texture, may measure up to 40 μm in thickness (Pl. 25, fig. 1). It is succeeded by an orthodoxly stacked secondary layer, composed of fibres on average 10 μm wide. Puncta up to 25 μm in diameter permeate both shell layers (Pl. 25, fig. 2), but no perforate canopies covering the distal ends of canals, as were found in *S. walcotti*, could be detected. The interior of the pedicle valve of *Crenispirifer* is divided medially by a high septum which like an identical structure in *S. walcotti* must have functioned as a muscle-attachment area. In transverse sections through the septum, narrow zones of small irregular myotest fibres can be traced running from base to apex on both sides to meet dorsally. The structure of the overlapping growth lamellae of *Crenispirifer*, which are formed as a result of periodic mantle retractions, differs in some respects from that of the overlapping growth lamellae described for *S. walcotti*. In *Spiriferina* the tip of the mantle lobe after the initial withdrawal began to deposit a series of horizontal, overlapping, organic and inorganic layers, but in *Crenispirifer* mantle regression was followed only by deposition roughly normal to the posteriorly inclined regression plane which preceded a return to normal primary and secondary shell deposition.

In summary, the shell structures of *Crenispirifer*, *Punctospirifer* and *Spiriferina cristata* are closely comparable with the standard shell succession of *Spiriferina walcotti*. No tertiary layer has been found in any Spiriferinacea.

(v) *Reticulariacea*

Unlike most forms assigned to the Spiriferidina, the Reticulariacea are generally recognized by being relatively smooth-shelled with rounded cardinal extremities and a short hinge line. Two species of *Phricodothyris* and one badly altered *Martinia* were available for study.

Transverse sections through both valves of *Phricodothyris* sp. from the Finis Shale (Pennsylvanian) of Texas reveal a remarkably well-preserved calcareous shell succession comprising three distinct layers. The primary layer, which measures up to 40 μm in thickness, is normally massive but in certain areas the texture may become porous, accompanied by the development of a fine lineation disposed normal to the outer shell surface (Pl. 25, figs. 3, 4). The surface micro-ornament of *Phricodothyris* is distinctive and involves some disruption of the primary layer. It consists of a series of regularly spaced concentric growth lamellae, each terminating anteriorly in a row of fine double-barrelled spines. Unlike the hollow spines of *Spiriferina walcotti* which connect with the shell interior by means of narrow canals, those of *Phricodothyris* terminate within the primary layer. Invariably the spines were broken, leaving only sunken bases which appear in longitudinal section as shallow, cigar-shaped hollows infilled with secondary material (Pl. 25, fig. 3). The general structure and possible function of the spines have already been discussed by George (1932 : 529) and need not be considered further. Clearly the spines of any one lamella were built up rapidly in localized patches of the circumferential generative zone of outer epithelium situated at the shell edge whilst neighbouring cells were still involved in the deposition of the primary layer. As George points out, the caecal prolongations of the mantle incorporated within the spines must have become wholly dead matter before the secretion of the next succeeding lamella.

Since a tertiary layer is deposited over the greater part of the shell interior, the secondary layer is comparatively thin, being about 25 μm in depth overall. Close to the valve margins, the secondary layer attains a thickness of nearer 40 μm which may indicate that the secondary layer secretory zone within the outer epithelium widened with age. Fibres are orthodoxly stacked and measure about 12 to 15 μm in width (Pl. 25, fig. 4). The tertiary layer consists of straight-sided, vertically stacked crystals which measure up to 15 μm in width (Pl. 25, figs. 4, 5). The fabric of the tertiary layer of *Phricodothyris* is strikingly similar to that of *Gryphus* even to the extent of exhibiting a regular transverse depositional banding. The banding in *Phricodothyris* sp. from the Finis Shale has an average periodicity of 1·5 μm.

From around the periphery of each concentric growth lamella, a plane dips posteriorly inwards to define the isochronous surface upon which the normal secretory processes were interrupted (Pl. 25, fig. 3). Such zones of mantle retraction must have been relatively narrow and confined to the outermost shell margins because regression planes, defining the extent of the disruption, terminate within the secondary layer. Although the zone of change-over from secondary to tertiary shell deposition is located very close to the valve margins, as in *Gryphus*, the tertiary layer is not affected by mantle regressions. As a result, there is no interdigitation of secondary and tertiary layers as, for example, in *Choristites*.

The shell structure of *Phricodothyris* sp. from the Carboniferous Limestone Series of Braidwood, Lanarkshire, was found to be identical to that of the American species. The transverse tertiary layer banding, in this case, had an average periodicity of 1·2 μm (Pl. 25, fig. 6).

The shell of the only specimen of *Martinia* that was available for study was badly altered, but parts of the original fabric could still be recognized. The primary layer had exfoliated, but parts of the secondary layer and a thick tertiary layer were identified (Pl. 26, figs. 1, 2).

(e) *Thecospira*

Thecospira is an unusual spire-bearing brachiopod, small but oyster-like in appearance, with a variably deep, cup-shaped pedicle valve and relatively flat, lid-like brachial valve. On the pedicle valve exterior there occurs a flattened cementation scar. In recent years there has been some debate as to the precise systematic position of *Thecospira*. Rudwick (1968 : 349) and Baker (1970 : 84) regarded it as an

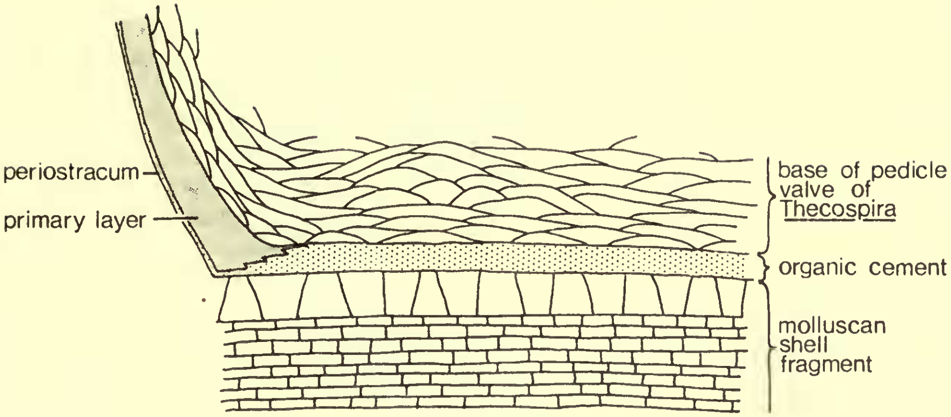

FIG. 19. Stylized section through part of the base of a pedicle valve of *Thecospira* cemented to a molluscan fragment, showing the inferred relationships between the organic cement, periostracum and primary layer.

aberrant strophomenide whereas Williams (1968a : 48 and 1972) argued convincingly in favour of a spiriferide identity for the genus. For precisely the same reasons as those put forward by Williams (1972) I regard *Thecospira* as a member of the Spiriferida.

The basic shell structure of *Thecospira* sp. collected from the St Cassian Beds (Triassic) of Northern Italy closely resembles that of *Spiriferina walcotti* (Sowerby) in that two calcareous shell layers are recognizable. An unusual aspect of growth of *Thecospira* is the absence of any recognizable primary layer within the cementation area of the pedicle valve. A complete specimen of *Thecospira* found cemented to a bivalve fragment was sectioned normal to the plane of attachment. In the brachial valve and in the convex, upstanding part of the pedicle valve, a primary layer measuring up to 25 μm in thickness was identified (Pl. 26, fig. 3), but below the attachment area a zone about 15 μm wide, infilled mainly with sediment, was found interposed between the flattened base of secondary layer fibres and the outer surface of the bivalve fragment (Pl. 26, fig. 5). Presumably this narrow zone was occupied during life by the organic adhesive which cemented the shell to the substrate (Text-fig. 19).

Since the initial secretory phase of newly proliferated cells comprising the outer mantle lobes of Recent brachiopods, both articulate and inarticulate, is known to involve the exudation of mucopolysaccharide, it is considered highly likely that a similar episode of organic deposition initiated the secretory regime of the thecospirid mantle. In the pedicle valve of *Crania anomala* Müller the cementing medium is the outer mucopolysaccharide layer (Williams and Wright 1970 : 18). The pedicle valves of living Thecideidina are presumably cemented to the substrate by a similar deposit, for mucopolysaccharide has been found as an impersistent external coating on the periostracum of *Thecidellina barretti* (Davidson) (Williams 1971b : 49). Since within the attachment area of the pedicle valve of *Thecospira* no primary layer is

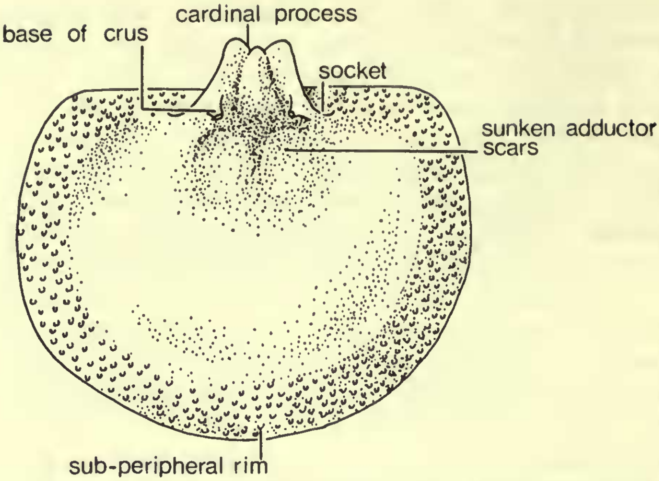

FIG. 20. View of the general morphology of the brachial valve interior of *Thecospira* (spiralium absent).

found, it seems likely that exudation of mucopolysaccharide and periostracum must have been sustained over a relatively broad zone of the outer mantle lobe. The suppression of the primary layer probably resulted from the persistent localized deposition of an organic pad internal to the periostracum which acted as a sufficiently rigid base and seeding sheet for the earliest-formed parts of secondary layer fibres.

Sections through both valves of *Thecospira* reveal that fibres of the secondary layer are orthodoxly stacked and measure, on average, 15 μm in width (Pl. 26, fig. 4). The interior of the brachial valve is not flat but sunken postero-medially in the vicinity of the dorsal adductor muscle scars and raised marginally as a tuberculate platform around the valve periphery (Text-fig. 20). A similar marginal tuberculate zone, forming a sub-peripheral rim, is known to occur in some thecideidines, including *Moorellina granulosa* (Moore) (Baker 1969 : 393). In radial sections through the brachial valve of *Thecospira*, each tubercle is found to comprise a cylindroid core of porous, non-fibrous calcite that protrudes above the surface of the rim and around which secondary layer fibres are deflected laterally and inwardly (Pl. 27, figs. 1, 2, 3, 4). Tubercles with solid cores of this sort measuring up to 60 μm in diameter closely resemble the pseudopuncta of certain Plectambonitacea and Gonambonitacea (Williams 1970 : 340). Pseudopunctation is also characteristic of the laminar shelled Strophomenida (Williams 1968a : 40), including all but the earliest Davidsoniacea. Yet the 'pseudopunctation' of *Thecospira* is much closer to that described for the spire-bearing *Cadomella*, the terebratulide *Megerlia* or more strikingly the Jurassic thecideidine *Moorellina* than it is for any of the earlier strophomenide or orthide stocks, for inwards of the sub-peripheral rim the tubercles are resorbed and overlapped by later secondary shell material. Submerged tubercles considered to have been functional peripherally are also found distributed sporadically within the secondary shell succession of the pedicle valve of *Thecospira*. The tubercles of both valves are not continuous with the primary layer as in *Moorellina* (Baker 1970 : 87), but arise as modifications of pre-existing secondary layer fibres.

Both punctate and impunctate specimens of *Thecospira* were collected from the same locality but whether or not they are variants of the same species has still to be established. The puncta occur as sediment-filled canals measuring up to 40 μm in diameter which permeate the primary and secondary shell layers (Pl. 27, figs. 4, 5). Whereas fibres are deflected towards the shell interior around tubercle cores, they are outwardly deflected around puncta.

In one punctate brachial valve of *Thecospira*, sections through the secondary layer revealed a series of at least six transverse micritic bands up to 10 μm thick which ran parallel with the inner shell surface and were outwardly deflected by puncta (Pl. 27, figs. 5, 6). The vertical spacing between bands is variable but generally measures about 10 μm to 20 μm. Since the bands are most prominent towards the inner surface and close to the valve periphery it is believed that they mark successive levels of organic layers which were sandwiched within the normal calcareous succession. Such periodic reversals to wholly organic exudation may have corresponded to temporary halts in shell growth, for fine overlapping growth lamellae do occur around the periphery of gerontic specimens. However, in the particular shell section which was found to exhibit a banded succession, individual growth lamellae could not be directly correlated with the micritic layers.

The dorsal and ventral myotests of *Thecospira* are composed of modified secondary layer fibres. The outlines of individual fibres are irregular and the lateral margins of adjacent fibres often occur welded together (Pl. 28, fig. 1). In the pedicle valve the arcuate anterior borders of the two ventral diductor scars are raised above the valve floor to form an anteriorly inclined overhang (Pl. 28, fig. 2). This semi-recumbent ridge is considered to have developed in response to the stresses placed on the overlying outer epithelium by the most anterior part of the ventral muscle base. It is evident that the angle between the shell surface and the estimated disposition of the long axes of muscle fibres in that region would approach more closely the most efficient maximum of 90 degrees (Text-fig. 21).

V. STRUCTURE OF THE BRACHIDIUM AND INFERRED DISPOSITIONS OF THE LOPHOPHORE IN SPIRIFERIDA

(a) Structure of spiralia

Within the order Spiriferida, the size, shape and disposition of the spiral brachidium that, in all probability, supported the lophophore are highly variable. In one of the earliest-known spiriferides, *Protozyga elongata* Cooper, support for the lophophore is rudimentary and consists simply of a pair of short prongs which extend anteriorly from a median connecting band, the jugum (Williams & Wright 1961 : 158, fig. 4g). When sectioned transversely close to the jugum, the calcareous outgrowths of *P. elongata* are found to be extremely slender. Sections through either branch reveal

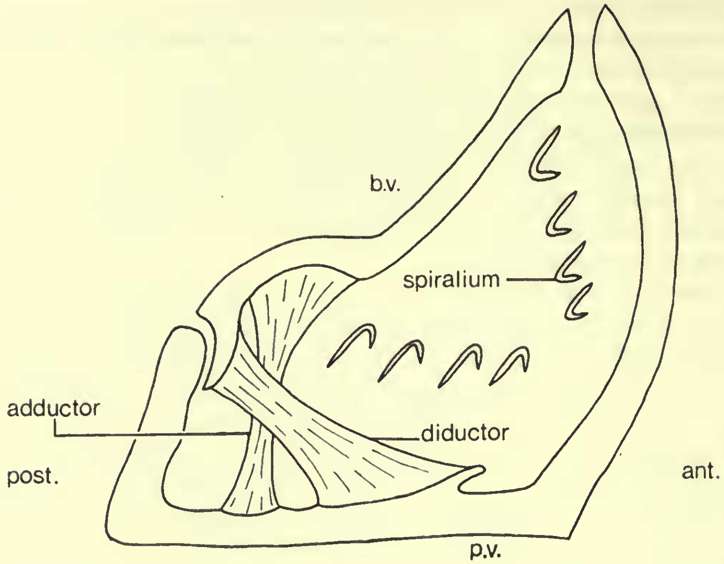

FIG. 21. Stylized longitudinal section through both valves of *Thecospira* showing the inferred dispositions of adductor and diductor muscles, and the U-shaped profiles of the spiral lamellae (b.v. – brachial valve, p.v. – pedicle valve).

outlines of only 25 to 30 secondary layer fibres stacked orthodoxly in rows up to five deep (Pl. 28, fig. 3). This compares with well over 1000 individual fibre outlines arranged in rows up to about 40 fibres deep occurring in any one transverse section through a spiral lamella of a mature *Spiriferina*. Due to secondary recrystallization, the precise attitude of the fibres comprising the brachidium of *P. elongata* could not be established with any degree of certainty.

In slightly younger representatives of the same stock, such as *Protozyga exigua* Hall which appeared in the late Ordovician (Rockland Formation), the anterior prolongations of the jugum extend further as a pair of narrow ribbons each coiling for up to one convolution, as a planispire aligned parallel to the median plane. Planispiral coiling of the brachidium in a plane parallel to the median plane is repeated and increased to 3 or 4 convolutions in the smooth Dayiacean, *Cyclospira*, although it is reported to be ajugate.

A number of late Ordovician and early Silurian genera characterized by the development of spiralia with medially directed apices are considered to have evolved from the primitive protozygid stock. These include *Catazyga, Zygospira, Idiospira* and *Glassia*. However in the majority of later Atrypacea, including *Atrypa*, the spiralia became reorientated dorso-medially with apices directed towards the midline of the brachial valve.

In almost all remaining Spiriferida, the apices of spiralia are directed laterally but in some genera, such as *Koninckina, Thecospira* and *Cyrtina*, the spiralia were directed ventrally or postero-ventrally. In a number of athyrididines, postero-median growth and bifurcation of the jugum resulted in the development of a pair of recurved arms (accessory lamellae) which were positioned adjacent to the innermost lamellae of the primary coils of the spiralia. In *Diplospirella* and certain allied genera continued growth of the accessory lamellae gave rise to a pair of intercoiled accessory spires which extended as far as the apices of the primary ones.

The structure and growth of the spiralia of *Spiriferina walcotti*, which may be considered as typical of many Spiriferida, have already been described (see p. 206). Secondary layer fibres which are generated in a zone running around the sharp outer edges of the spiralium are secreted on both sides of the spiral lamella and each fibre is seen to follow an arcuate path away from the apex of the spire which, it is believed, corresponds to a segment of a logarithmic spiral. In cross section, the convex keels of fibres arch outwards in both directions from a median plane (Text-fig. 7b). Similar double-sided spiral lamellae have been identified in the early atrypaceans *Catazyga headi* (Billings) (Pl. 28, fig. 4), *Idiospira thomsoni* Davidson (Pl. 28, figs. 5, 6), the dayiacean *Dayia navicula* (Sowerby) (Pl. 29, fig. 1), the early retziidine *Rhynchospirina maxwelli* Amsden (Pl. 29, fig. 2), the cyrtiacean *Ambocoelia umbonata* (Conrad) (Pl. 29, figs. 3, 4) and the spiriferaceans *Theodossia hungerfordi* (Hall) (Pl. 29, fig. 5), and *Spirifer trigonalis* Martin (Pl. 29, fig. 6). Spiralia belonging to the aforementioned genera, when sectioned, present a similar profile to that described for *Spiriferina*. The outward edge of each lamella is pointed whereas the inner edge is generally truncated. The thickest part of the lamella is around its mid-region. On either side of a line running from roughly the middle of the blunt inner edge to the fine outer edge, the convex keels of small regularly stacked secondary layer fibres, generally less than 10 μm in width, arch outwards. Narrow spines, which outwardly deflect localized groups of fibres, project from the median-facing side of the spiralia of *Idiospira* (Pl. 28, figs. 5, 6). Presumably these spines performed a similar function, and were deposited in a similar manner, to those projecting from parts of the spiralia of *Spiriferina*.

The structure of the spiralia of certain Athyrididina differs markedly from the structure of those previously described. Instead of exhibiting a double-sided growth pattern, sections through the athyrididine spiralia reveal deposition of secondary layer fibres on only the median-facing side of each lamella. As spiralia were generally embedded in rock matrix enclosed within both valves of each specimen, it was not possible to view surfaces of lamellae directly to establish the precise orientation of fibres. However, this could be deduced by preparing two vertical transverse sections which cut tangentially through the edges of the spiralia (Text-fig. 22a), once on its anterior side and once on its posterior side, and then noting the relative disposition of fibres in each section (Text-fig. 22b). In the anterior section, fibres are directed dorsally whereas in the posterior section they are directed ventrally. Progressive changes in the cross-sectional outlines of fibres between the dorsal and ventral extremities of each sectioned lamella are considered to reflect corresponding changes in the orientation of fibres from one end to the other. The observed pattern of sectioned fibres corresponds to that occurring in one half of a sectioned 'double-sided' spiral, such as in *Spiriferina*, and clearly reflects for each individual skeletal unit a

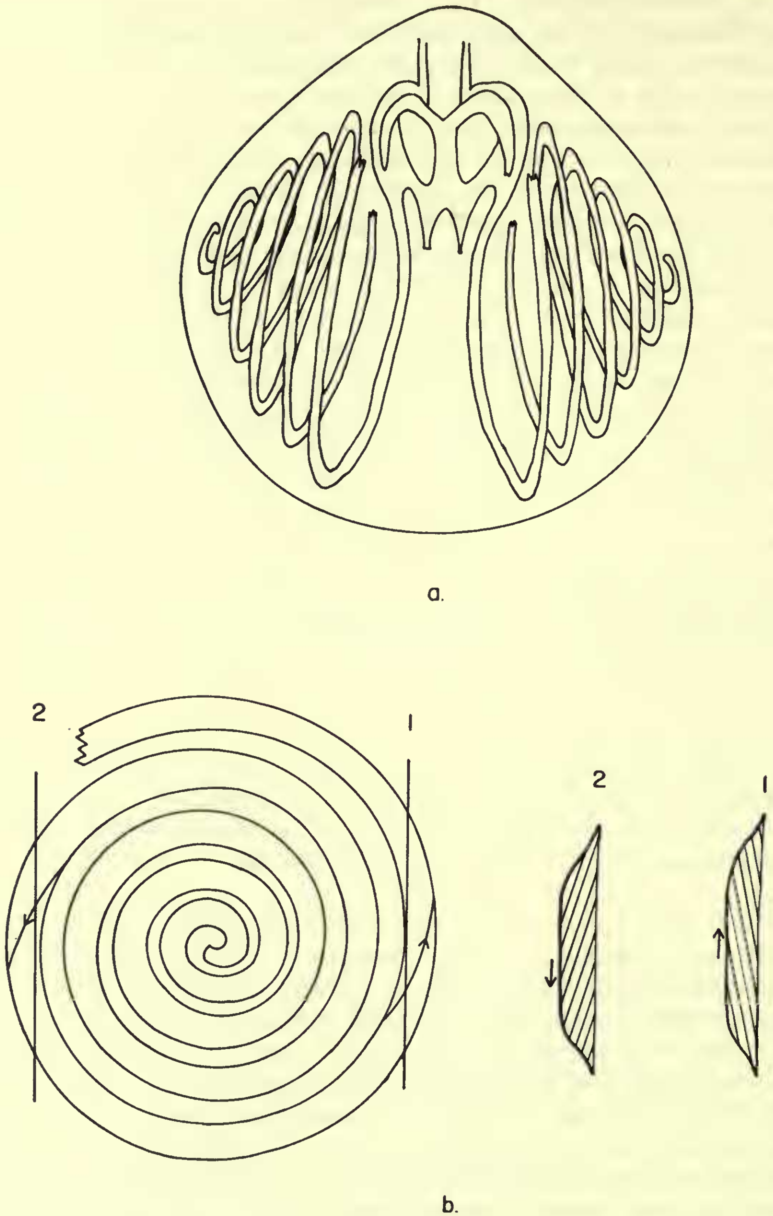

FIG. 22. a. Generalized plan view of an athyrid spiralium. The two lines of section are located on either side of the axis of the spiralium. Consecutive coils of each spire are not planar but curved so as to appear outwardly concave. b. Lateral view of a spire showing the lines of section and the growth direction of fibres. In the anterior section (1) fibres are directed dorsally whereas in the posterior section (2) fibres are directed ventrally.

similar pattern of fibre growth. Since each spiral lamella grew by accretion of secondary layer material on only the median-facing side, it is evident that resorptive processes must have operated on the apical side. Although the arrangement of growth and resorption faces is contrary to what might be expected, a steady overall increase in the size of the spiralia can still be achieved dependent on the attitude of the lamellae. Consecutive coils of the spiralia of many athyrididines are not planar but curved so as to appear outwardly concave. In consequence the terminal faces of fibres deposited on the median-facing side of both spires are directed outwards away from the median plane.

'Single-sided' spiral lamellae have been identified in the athyridaceans *Composita ambigua* (Sowerby) (Pl. 30, figs. 1, 2), *Athyris spiriferoides* (Eaton) (Pl. 30, fig. 3), *Diplospirella wissmani* (Münster) (Pl. 30, fig. 4) and *Anisactinella quadriplecta* (Münster) (Pl. 30, fig. 5), as well as other more distantly related forms including *Koninckina leonhardi* (Wissman) (Pl. 30, fig. 6 ; Pl. 31, fig. 1), *Amphiclina amoena* Bittner (Pl. 31, fig. 2) and *Thecospira* sp. (Pl. 31, fig. 3).

Compared with secondary layer fibres found elsewhere in the brachial valve, those comprising the spiralia of *Diplospirella* and *Anisactinella* are abnormally small. On both primary and accessory lamellae fibres measure, on average, 12 μm in width as opposed to 60 μm width on the floor of each brachial and pedicle valve. The accessory lamellae as well as the primary lamellae of *Diplospirella* and *Anisactinella* are characterized by one-sided growth, although the convex keels of fibres arch outwards towards the apices of the spiralia and not medially as on the main spires (Text-fig. 23). Since each coil of the accessory lamellae is situated lateral to the corresponding coils of the primary lamellae it is evident that two non-depositional faces are in opposition to one another throughout. Both primary and accessory lamellae are fimbriate but as yet it has not been established whether the fimbriae occur on only the anterior-facing edges of the spires, as in *Spiriferina*. Nevertheless, presumably they served a similar purpose. The spinous outgrowths are found to project from only the median-facing side of primary lamellae and the apical side of accessory lamellae. On the opposite sides of both sets of lamellae, spine bases are resorbed along with the long exposed trails of fibres comprising the rest of that surface.

Although parts of the calcareous lophophore supports of some living Terebratulida are known to be fimbriate, the relationships between fimbriae and adjacent soft tissues, as well as modes of secretion, have yet to be established. At high magnifications, the distal extremities of spines projecting from the spiralia of *Diplospirella* are noticeably jagged, resembling in shape the thorns of a rosebush. Such products of mineral deposition are totally foreign to mature outer epithelial cells which are normally involved in the build-up of more conventional secondary shell material, but some elements of spicular skeletons, known to be secreted within the lophophore and mantle of a number of living Terebratulida, bear resemblance to the jagged parts of spines. Spicules, however, are found only within the inner epithelium and connective tissue where, according to Williams (1968b : 280), they develop within scleroblasts. Assuming that the primary and accessory spiralia of *Diplospirella* were ensheathed by connective tissue and inner epithelium of the lophophore, the 'raw materials' for spicule formation were certainly available. However, to become embedded within the secondary shell succession of the spiralia, spines secreted by mesoderm or endoderm must first have pierced the outer epithelial lining, which seems unlikely. More probably, the spines were secreted by specialized outer epithelial cells reminiscent in structure and function of those which must have contributed to the formation of solid tubercle cores or taleolae in other genera.

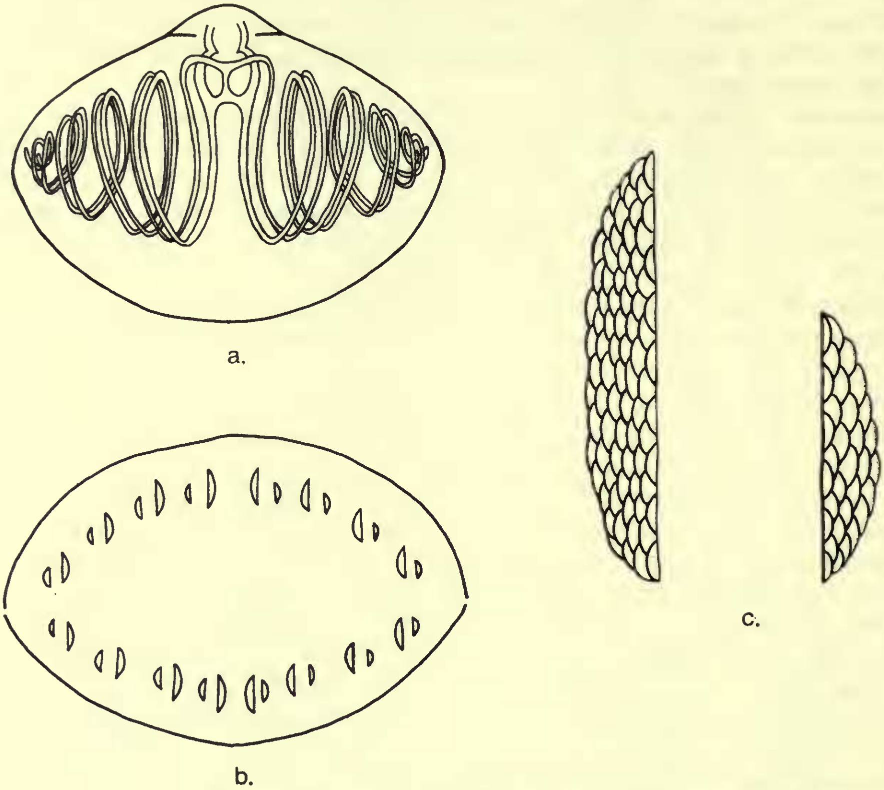

Fig. 23. a. View of the spiral brachidium of *Diplospirella wissmani* showing the disposition of the primary and accessory lamellae. b. Transverse section through both valves and spiralium of *Diplospirella*. c. More detailed view of a transverse section through a primary (left) and accessory (right) lamella of *Diplospirella* showing the shape and stacking of secondary layer fibres.

In Koninckinacea, the brachidium consists of a pair of double spires with the principal pair arising on a simple crural process from which they diverge at a sharp angle. A jugum is formed by the anterior extension and union of the crural processes, and the accessory spires which originate on this connecting band lie ventral to the main pair and are co-extensive with them. The apices of both pairs of spiralia are directed towards the lateral slopes of the pedicle valve (Text-fig. 24a, b).

By comparison with the giant-sized fibres which make up the general shell succession of *Koninckina*, the fibres composing the spiral brachidia are small (on average

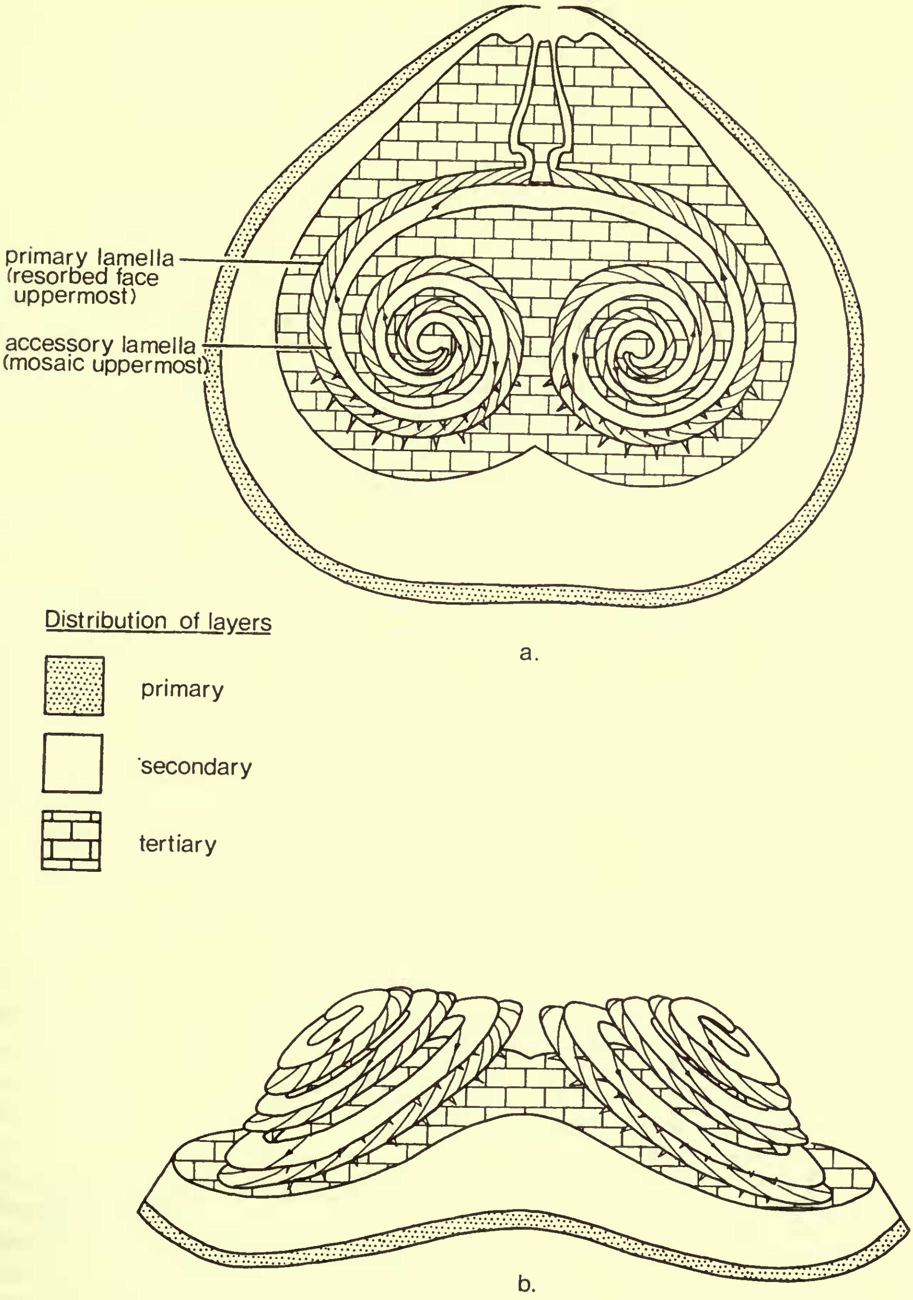
primary lamella (resorbed face uppermost)
accessory lamella (mosaic uppermost)
Distribution of layers
primary
secondary
tertiary
a.
b.

FIG. 24. Plan view (a) and anterior view (b) of a generalized koninckinacean brachial valve interior showing the disposition of the spiralium (including growth vectors of fibres) and the distribution of shell layers.

about 7 μm wide). The size range of those fibres in the brachial structures, however, compares more favourably with that of fibres occurring in other articulates such as *Retzia* sp., even from the same horizon, in which mature secondary layer fibres are about 10 μm wide. As previously mentioned, fibres composing the spiralia of *Diplospirella* and related genera are about a fifth the size of those occurring elsewhere in both valves.

Transverse sections through the arms of the koninckinacean spiralium reveal something of the size, shape and stacking of its constituent fibres (Pl. 30, fig. 6 ; Pl. 31, fig. 1). Fibre outlines associated with such structures appear much more conventional than those of the rest of the shell in that they display easily recognizable keels and saddles. This configuration provides a convenient means of recognizing growth surfaces, since the convex surfaces of keels always face towards a depositional surface. In *Koninckina* the regular overlapping habit of fibres in sections through spires indicate that deposition took place on the dorsal surface of the primary lamellae and on the ventral surface of the accessory lamellae. The two inner opposing faces of the primary and accessory lamellae were thus surfaces of resorption.

Whilst examining specimens of *Amphiclina*, a disarticulated pedicle valve was found which retained part of a primary lamella still located in almost the exact position of growth (see Pl. 16, fig. 3). The ventral-facing (resorbed) side was uppermost. Nevertheless, despite the lack of any recognizable mosaic, it was possible to plot the long axes of exposed trails of fibres, and by using them as growth vectors, thereby reconstruct an overall brachidial growth pattern. The fibres comprising each spiral lamella curve obliquely across its surface (Pl. 31, fig. 2 ; Text-fig. 24), from inner to outer edge, like those of *Spiriferina*, in such a way that their trails inscribe a spiral curve (probably logarithmic) on which the terminal parts of fibres are directed progressively further away from the apex of the spire to produce a gradual peripheral expansion along the outer edge of every whorl. On the outer half of the ventral side of the primary lamella, the oblique outlines of exposed trails are replaced by a much finer lineation aligned at right angles to the outer edge of the lamella. At high magnification (Pl. 31, fig. 4), the lineation appears as a series of narrow troughs and ridges, on average 4 μm wide. No comparable features have, as yet, been recognized on any other articulate brachiopod so that the mode of formation and function of such lineations are problematical. However, it seems likely that they may be the product of some unusual resorptive process. Both primary and accessory lamellae of koninckinaceans are fimbriate, in the sense that fine spines project obliquely from their depositional surfaces and cause the trails of surrounding fibres to be gently deflected around them.

The form of spiral brachidium that is characteristic of *Thecospira* differs markedly from that found in all other Spiriferida. A comprehensive description of the macroscopic morphology of the thecospirid brachidium has been given by Rudwick (1968 : 337) and needs only to be referred to briefly. From the base of the cardinal process, a pair of short crura extends anteriorly to join with, and support, the ventrally directed spiralia. According to Rudwick, a simple transverse jugum connects the proximal ends of the crura. Each lamella is U-shaped in section (Text-fig. 21) with the dorsal branch being thicker and about twice as long as the ventral one. The two branches close inwardly on the side closest to the spiral axis, so that the groove faces laterally outwards.

At the microscopic level, the dorsal limb of the U is found to comprise small, orthodox secondary layer fibres which measure, on average, 8 μm in width, but the lower limb is essentially non-fibrous (Pl. 32). The convex keels of fibres in the upper limb face ventrally into the groove and towards the lower limb. In cross section the profile of the lower limb is undulating in such a manner as to suggest, in three dimensions, that it is fluted parallel or subparallel to the length of the spire. This interpretation is further supported by the occurrence of a series of concentrically banded zones, each about 20 μm wide, which coincide with the undulations (Pl. 31, fig. 5). The narrowest diameters of the concentric bands are so fine that it seems most likely that the zones terminate distally as sharp points. If this is the case, then the undulations may be considered as sections through laterally fused spinose outgrowths which project obliquely outwards from the lower limb of the U-shaped groove.

At the junction of the upper and lower limbs the secondary layer fibres are bent round through 180 degrees so that their curved saddles come to rest against the inner surface of the lower limb. At the opposite, outer edge of the upper lamella, fibres are deflected around spine bases. Since peripheral spine bases have been recognized in every section through the spiralia of *Thecospira* that has been examined, they must be densely distributed in that area. Fibres of the upper limb are also disturbed within a variably wide non-fibrous zone which runs from midway along the ventral surface, obliquely inwards, and terminates on the dorsal surface just above the junction of the upper and lower limbs of the U. In some sections, the enclosed accretions are fairly massive, but in others they are much less prominent. Small concentrically banded zones have been recognized within some of these, and may represent parts of embedded spines (Pl. 31, fig. 6). Since no similar deposits have been recognized within the brachidia of other fossil or Recent brachiopods, they are extremely difficult to interpret mainly because any sediment-free fragments of spires on which a three-dimensional reconstruction could be based are lacking. Once suitable specimens are found a more enlightened explanation may be forthcoming. At present, the only objects that can be considered as likely to give rise in section to such amorphous shapes are forms of spicules such as are found within the lophophore and mantle of some living Terebratulida.

Sections cut through the middle of spiral coils reveal transverse outlines of fibres but tangential sections show successions of long trails of fibres. If the shape of sectioned fibres can be taken as a rough guide to their orientation, then it is evident that the fibres comprising the upper limbs of the grooved spiral lamellae are aligned sub-parallel to the curved edges of the spiralia. This is essentially the same pattern as that observed in more conventional spiralia (equiangular spiral growth), thus it is assumed that the spiral lamellae of *Thecospira* grew in the same way.

(b) Inferred dispositions of the spiriferide lophophore

The relationships between skeletal supports and brachial appendages have been investigated in living Terebratulida with a view to establishing the most likely dispositions of the lophophore in extinct Spiriferida. In living long-looped forms, such as *Macandrevia*, the lateral arms of the plectolophous lophophore are supported by the ascending and descending branches of the calcareous loop (Text-fig. 25).

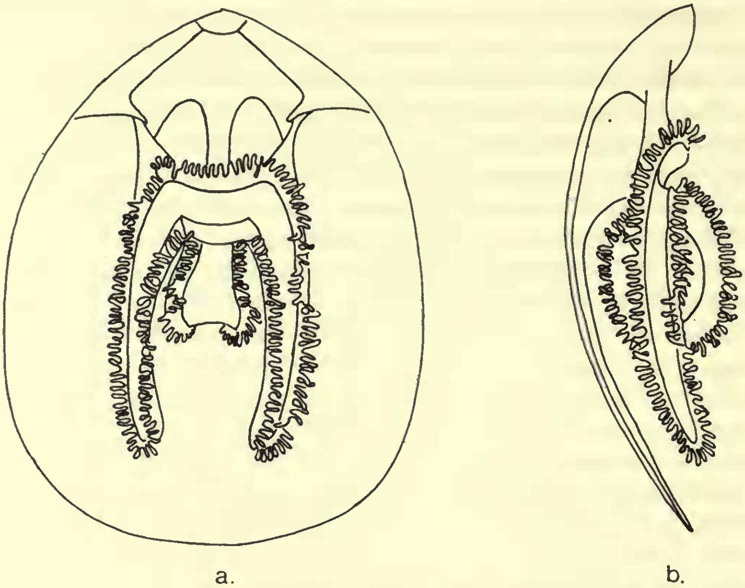

FIG. 25. Ventral (a) and lateral (b) views of the plectolophe of *Macandrevia* and its calcareous supports.

They bear a double brachial fold, two rows of paired filaments, and are served by two brachial canals (Williams 1956 : 263). As both canals are tucked in between the ascending and descending branches of the loop, it is of interest to note that opposing faces of the calcareous support of each side-arm bear surfaces of resorption while those on outward-facing sides bear surfaces of growth which exhibit a well-developed secondary shell mosaic. When viewed in section, the convex keels of fibres comprising the ascending and descending branches are seen to arch outwards away from each other (Text-fig. 26). Since exactly the same relationship exists between fibres comprising the primary and accessory lamellae of *Diplospirella* and *Koninckina* it seems reasonable to assume that the brachial canals of these extinct genera must also have occupied a median position between the two lamellae. Thus in more normal athyrididines in which the accessory lamellae are greatly reduced or non-existent, the brachial canals of the lophophore must have been situated on the apical sides of the primary lamellae. By using the one-sided distribution of spinose outgrowths (fimbriae) as a means of determining the position of the lophophore, Rudwick (1960a : 375) arrived at the same conclusion. Since the double-sided spiral lamellae of most other Spiriferida also bear spines on their median-facing sides, Rudwick considered that they too possessed brachial systems orientated with the main body of the lophophore situated on the apical sides of lamellae. Certainly in those forms which

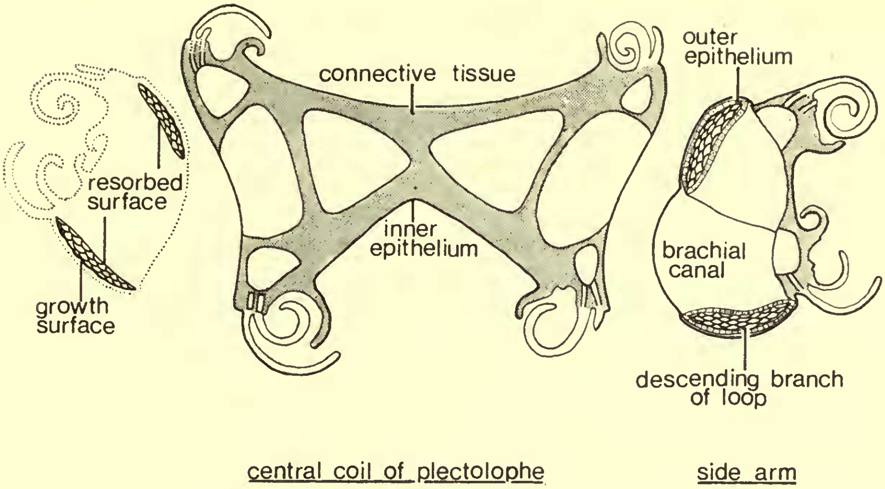

FIG. 26. Stylized transverse section through part of the plectolophe of *Macandrevia* showing the relationship of soft parts to the growth and resorbed surfaces of the ascending and descending branches of the loop. (After Williams, 1956 : text-fig. 4.)

show the greatest swelling in the median regions of lamellae, such as *Spirifer trigonalis*, the greater part of the swelling is on the apical side. In addition, since the width of the lamella is greatly reduced in its inner half, behind the swelling, partial resorption must have operated on some parts of that side. Thus the disposition of the brachial canals can still be correlated with areas of resorption on double-sided lamellae. In *Thecospira*, the inferred disposition of the lophophore, as deduced by this method, contradicts the hitherto perfectly plausible views expressed by previous authors (e.g. Rudwick 1968 : 335, fig. 3B). Placed against the surface undergoing resorption the main body (or brachial axis) of the lophophore would have rested on the dorsal surface of the broad fibrous limb of the U-shaped lamellae, and not within the groove. The precise orientations of the brachial groove(s) and filaments which comprised the food-gathering apparatus of the lophophore are less easy to decipher and, regrettably, ultrastructural studies relating to brachidial structure shed little new light on this tantalizing problem. Whether the spiriferid brachidium supported a simple spirolophe (Rudwick 1960a, b) with only a single set of filaments and one food groove, or a doubled set of appendages, the deuterolophe (Williams 1956 : 270, 1960 : 515 ; Williams & Wright 1961 : 149-176) is still open to discussion. However, since spiral brachidia may be divided into two separate groups based principally on the recognition of single or double-sided growth patterns, it may well have been that a genuine diversity in brachial structure existed. By analogy with the side-arms of long-looped terebratulides, the twin coils of spiralia belonging to forms such as *Diplospirella* and *Koninckina* may have supported a double row of paired filaments. If so, the single spiral coils of other athyrididines may also have provided a lesser support for the same system. On the other hand, spiral brachidia exhibiting double-sided growth may have supported single spirolophes, especially in those forms which appear to be without a jugum as in a number of cases.

VI. CONCLUSIONS

Recent research has shown that, in all probability, the secretory regime of articulate and inarticulate brachiopods has always involved at least three fundamental operations. Certainly in all forms of living brachiopods yet studied at the ultrastructural level (including Craniacea, Rhynchonellida, Terebratulida and Thecideidina) deposition of an outer mucopolysaccharide cover and an inner fibrillar triple-layered membrane has preceded secretion of the predominantly mineralized part of the exoskeleton. Presumably these two organic constituents comprised part, if not all, of the periostracal covering to the calcareous exoskeleton of the primitive *Protozyga*-like stock which is considered as ancestral to all Spiriferida (Text-fig. 27). If similarities in shell structure between *Protozyga* and contemporary Rhynchonellida are of any significance in indicating a common ancestor, then the earliest representatives of the Spiriferida almost certainly had only two calcareous shell layers. By the beginning of Silurian times, however, the secretory regime of most Spiriferida had developed further giving rise to three main types of skeletal fabric. The first, which includes the Atrypacea, Dayiacea, early Athyridacea and some early Spiriferacea, was characterized by being impunctate and possessing a variably thick tertiary prismatic layer in addition to the standard primary and secondary layers. The second group, including the Retziacea and Suessiacea, which were both punctate, possessed only primary and secondary shell layers. The third group, including the Cyrtiacea and remaining Spiriferacea, was the most conservative and secreted impunctate shells consisting only of primary and secondary layers.

Throughout the remainder of spiriferide evolution such clear-cut distinctions were not maintained. As far as is known all Atrypidina possessed three calcareous shell layers, but, unlike the Meristellidae, few later Athyridacea appear to have secreted a tertiary layer. *Cleiothyridina* is the only known Carboniferous athyrid to have done so. The Triassic Diplospirellinae are characterized by an exceedingly coarse fibrous secondary layer, but no additional tertiary layer deposit like that found in contemporary and younger Koninckinacea is present. The exoskeletal succession of the Retziacea was remarkably stable from Silurian to Triassic times. The impunctate Cyrtiacea and punctate Suessiacea were equally conservative. Considerable variation is shown, however, within the remainder of the Spiriferidina. As far as is known, nearly all Devonian Spiriferacea possessed only primary and secondary layers but later stocks show greater diversity. Punctation was developed in at least two stocks, the Spiriferinacea and Syringothyridae, and tertiary prismatic layers are found in some Carboniferous Spiriferidae and Brachythyrididae. In the Reticulariacea, too, a tertiary layer was deposited. Tubercles with non-fibrous cores grew peripherally in punctate and impunctate Thecospiridae and some Koninckinacea, but away from the shell edge they ceased to become functional and were submerged within later-formed parts of the calcareous succession. In this respect, such rod-like bodies differ from the pseudopuncta of Strophomenida with which they have, in the past, been compared and no special phylogenetic significance is attached to their appearance.

From the foregoing account, it is evident that despite the great diversity of form that has accompanied spiriferide evolution, there were few radical changes in

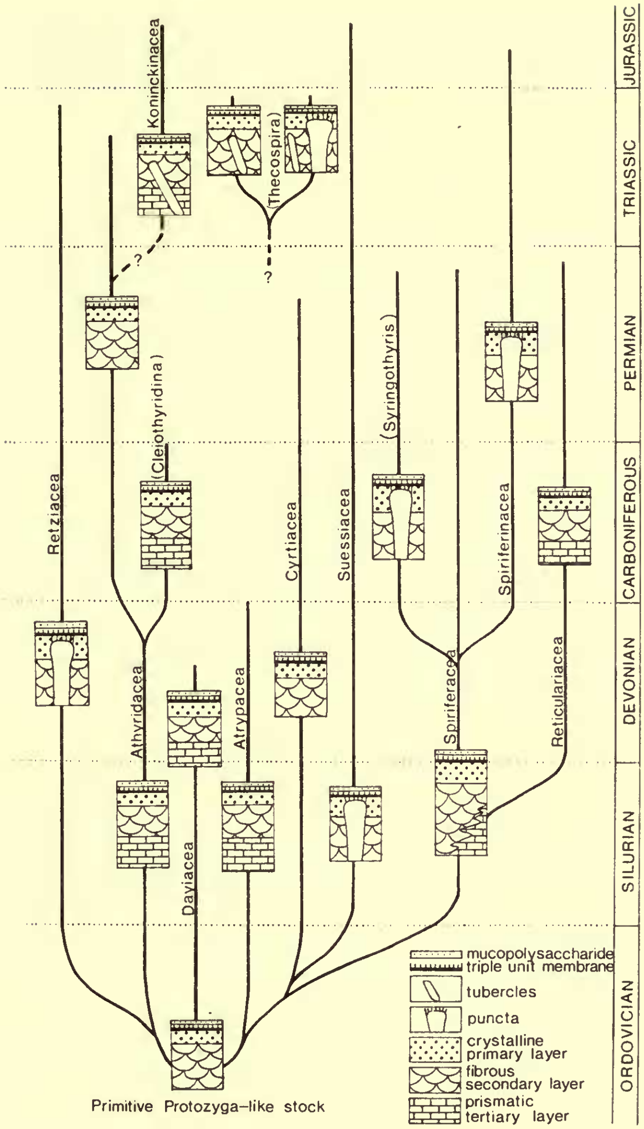

FIG. 27. Inferred phylogeny of the skeletal successions of the Spiriferida.

secretory regime. In *Spiriferina walcotti* (Sowerby), which has been selected as a standard model for spiriferide shell deposition, and in living Terebratulida, the structure of the primary and secondary layers and the finer details of shell punctation are very similar. Clearly the spiriferide outer epithelium was little different from that found in most living articulates. Even in forms possessing a tertiary layer, the nature of the outer epithelium may be reasonably inferred on account of a similar layer occurring in the living terebratulide *Gryphus vitreus* (Born). Indeed, all basic mantle secretory processes that are known to have operated in spire-bearing Brachiopoda, from their appearance in the Ordovician to their extinction in the Jurassic, were successful enough to have been retained by living articulate brachiopods of one form or another.

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